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Do aeolian deposits and sand encroachment intensity shape patterns of vegetation diversity and plant functional traits in desert pavements?

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Abstract: The effects of sand encroachment on composition, diversity, and functional patterns of vegetation in drylands are rarely studied, and yet addressing these aspects is important to deepen our understanding of the biodiversity conservation. This study aimed to investigate the effect of sand encroachment on plant functional biodiversity of desert pavements (gravel deserts) in the Sahara Desert of Algeria. Plants were sampled and analyzed in three desert pavements with different levels of sand encroachment (LSE) and quantity of aeolian deposits (low, LLSE; medium, MLSE; and high, HLSE). Within the sample-plot area (100 m²), density of every plant species was identified and total vegetation cover was determined. Plant taxonomic and functional diversity were analyzed and compared between LSE. Result showed that 19 plant species in desert pavements were classified into 18 genera and 13 families. Asteraceae and Poaceae were the most important families. The species *Anabasis articulata* (Forssk) Moq. characterized LLSE desert pavements with 11 species, whereas *Thymelaea microphylla* Coss. & Durieu ex Meisn. and *Calobota saharae* (C&D) Boatwr. & van Wyk were dominant species of desert pavements with MLSE (14 species) and HLSE (10 species), respectively. The highest values of species richness and biodiversity were recorded in desert pavements with MLSE, while low values of these ecological parameters were obtained in desert pavements with HLSE. Desert pavements with LLSE were characterized with the highest values of species abundances. Plant communities were dominated by chamaephytes, anemochorous, arido-active, and competitive stress-tolerant plants. The increase in LSE along the gradient from LLSE to HLSE induced significant changes in plant community variables including decreases in plant density, plant rarity, lifeform composition, morphological type, and aridity adaptation. Desert pavements with HLSE favor the degradation of vegetation and trigger biodiversity erosion.

Keywords: desert pavements; hot and arid rangeland; plant diversity; land degradation; sand encroachment; plant functional trait; Sahara Desert

1   Introduction

Drylands, in their different regimes of aridity, account for more than 40% of the global land surface, and are extending due to global warming (Fu and Fung, 2014; Peguero-Pina et al., 2020). The Sahara Desert is not only the largest hot desert worldwide, but also the most typical desert for its extreme aridity. This ecoregion is characterized by prolonged periods of drought and special flora with remarkable adaptations (Ozenda, 1991). According to Bouallala et al. (2020), landscapes with different geomorphology exist in the Sahara Desert, including erg and sandy soils, gravel deserts, stony and clayey substrate, rocky lands, mountain range, depressions, nabkhas, wadis with or without saline soil, wetlands, and oases. Among these landscapes, desert pavements are widespread and most common (Bouallala et al., 2022). Parsons and Abrahams (2009) define a desert pavement as a flat desert surface covered with closely packed, interlocking angular or rounded rock fragments of pebble and cobble size. A desert pavement is a gravel desert also called "Reg" in western Sahara region.

Sand encroachment is one of the phenomena of hot and arid environments (Yazdani et al., 2020; Bouchlaghem et al., 2021; Dashti et al., 2021). It is the consequence of a complex phenomenon resulting from multiple causes and manifests in different ways, including sand tearing, aeolian transportation, deposit, and accumulation to build different forms of dunes (FAO, 2014; Bouarfa and Bellal, 2018). The effect of wind is the major reason in drylands (Bouzekri et al., 2023). This natural factor can selectively erode the fine particles and remove them, and can accumulate several meters downwind, causing severe sand encroachment problems (Al-Dousari et al., 2019; Chenchouni et al., 2019, 2022), without neglecting the anthropogenic perturbations that contribute to aggravate the consequence of sand encroachment (Al-Dousari et al., 2019). One of the repercussions of sand encroachment in drylands is the erosion of both land and phytogenetic resources with multiple uses (medicinal, food, energy, industrial, etc.) (Bradai et al., 2015), knowing that hundreds of hectares of land are lost each year due to desertification (Benabderrahmane and Chenchouni, 2010) and different forms of erosion (Arar and Chenchouni, 2012, 2014; Neffar et al., 2018; Bouzekri et al., 2023).

Land degradation resulting from sand encroachment in desert habitats represents a serious challenge to the sustainability of ecosystem functioning, especially since these xeric species are known for their vulnerability to climate change combined with the increase in intensity of anthropogenic disturbances, which can lead to a decrease in ecosystem services provided by various natural resources (Copeland et al., 2017; Kouba et al., 2021; Macheroum and Chenchouni, 2022). Moreover, it has been reported by Shameem et al. (2017) that the magnitudes of natural and human disturbances can be the drivers of changes in species diversity in plant communities.

The vegetation of different geomorphological formations of the Sahara Desert has been widely surveyed (Lemee, 1953; Quézel, 1965; Monod, 1992; Benhouhou et al., 2001; Coude-Gaussen, 2002; Chehma, 2005; Fabre, 2005; Bouallala, 2013; Bouallala et al., 2020). Some investigations of the Sahara Desert have assessed the carrying capacity of camel in desert rangelands (Chehma, 2005; Bouallala, 2013). Previous climatological (Seltzer, 1946; Dubief, 1959, Dubief, 1963, Le Houérou, 1990) and vegetation studies of this ecoregion have highlighted the low and irregular precipitation, large thermal ranges, strong evaporation, and frequent and intense winds. These factors act seasonally on the dynamics of sandy formations, and consequently on the dynamics and structure of vegetation under different levels of sand encroachment (LSE), although plant survival in drylands is affected by the combination of high solar radiation, high temperatures, low relative humidity, and scarcity of available water (Peguero-Pina et al., 2020).

As the movement of sands is a characteristic phenomenon of hyper-arid environments (Sinsin et al., 2021), its effects on the plant component remain little studied and poorly understood. The studies related to this topic have focused on the composition, community structure, and functional traits of plants in the Sahara Desert (Chenchouni, 2012; Bradai et al., 2015; Bouallala et al., 2020; Azizi et al., 2021). However, these is no study about plant community composition and functional diversity in relation with LSE. This work addressed and examined the relationships of vegetation

diversity and plant functional attributes with LSE in desert pavements at northern Sahara Desert. This study aimed to answer the following questions: (1) do the floristic composition and plant diversity parameters vary according to LSE in desert pavements? (2) what are and which functional traits predominate in this xeric environment? and (3) is there a relationship of plant functional traits, composition, and diversity parameters with LSE?

2 Materials and methods

2.1 Study area

The region of El-Guerrara is located 115 km northeast of the Ghardaia Province in the Sahara Desert of Algeria (Fig. 1). The climate of this region is hot and hyper-arid (de Martonne aridity index=1), where the dry season lasts all the year. The annual precipitation totals 40.0 mm with precipitation deficit of 1639.0 mm/a (Table S1). The coldest month is January (annual mean temperature is 4.4°C (±3.2°C)) and the warmest month is July with the maximum temperature of 42.7°C (±4.6°C), and potential evapotranspiration (PET) peaked at 233.9 (±20.3) mm. The annual average of PET was 139.9 (±19.3) mm (Table S2). The main agricultural activity in the Sahara Desert is date palm cultivation, which is expanding in space and increasing over time (Mihi et al., 2019a, b). Recently other vegetables and industrial crops are grown in the understory of date palm and in new exploited lands. Rocky and sandy soils predominate with a very low or even zero organic matter (Dadamoussa et al., 2015). The dominant soil is lithic leptosol (Dewitte et al., 2013).
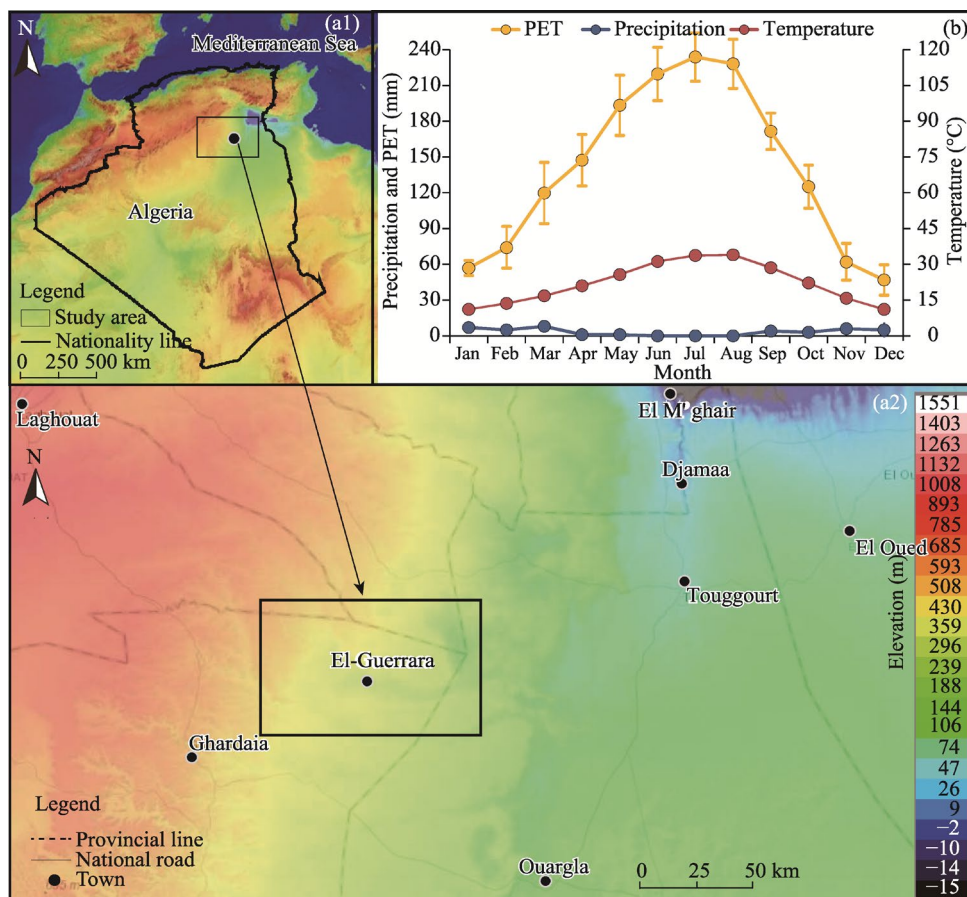

Fig. 1 Geographic location and elevation (a1 and a2) of the El-Guerrara region (Ghardaia Province, Algeria), and monthly meteorological data for mean temperature, precipitation, and potential evapotranspiration (PET; b). Bars are standard errors.

2.2   Plant sampling, data collection, and analysis

At the El-Guerrara region (Fig. 1), plants were sampled within three desert pavements, representing different LSE and quantities of aeolian deposits: (1) low LSE (LLSE): presence of aeolian sand ripples less than 5 cm tall; (2) moderate LSE (MLSE): presence of sand ripples and small nabkhas less than 50 cm tall, and (3) high LSE (HLSE): presence of aeolian sand ripples (<5 cm tall), small dunes (<50 cm tall), and bushy nabkhas less than 2 m tall. Plants were sampled during the period of plant growth (February–April) of 2015, with five replicates per site. In each sample plot, plant density was determined within an area of 100 m^2 (Chehma, 2005; Bouallala, 2013). Vegetation cover was also estimated inside the same sampling plots by computing the proportion of horizontal vegetated area occupied by the vertical projection of plant canopy. Species identification was referenced from Quézel and Santa (1962, 1963) and Ozenda (2004). Researchers updated the list of plants according to the African plants database (http://www.ville-ge.ch/ musinfo/bd/cjb/africa/recherche.php).

2.3   Analysis of plant diversity

2.3.1   Composition and classification of plant diversity

For the entire study area and for each LSE, plant traits and taxonomic diversity were assessed by calculating the following parameters: vegetation cover (VC) as mean of samples of LSE, density (N') was determined as sum of species abundances per LSE, relative abundance (RA) computed as the proportion of species abundance to the total abundances of all species per LSE, species richness (S) consisted of the total number of species identified in each sampling plot and LSE, average of species abundance ($N':S$ ratio) defined as the average number of individuals per species, average of species cover (VC:S ratio) established as the average vegetation cover per species, average of individual cover (VC:N' ratio) defined as the average vegetation cover per individual, occurrence (Occ) was calculated for each species by the number of samples in which the species occurred/total number of samples. Four classes of Occ were distinguished: very accidental species (Vac) with occurrence <10% in samples, accidental species (Acc) having occurrences ranging from 10% to 25%, common species (Cmt) are present in 25%–50% of samples, and constant species (Cst) with occurrence equals to 50% or more (Neffar et al., 2016). Two diversity indices (Shannon's diversity index and Simpson's diversity index), and one evenness index (Pielou's evenness) were computed in this study. Shannon's diversity index (H') was the most frequently used index compared with other diversity indices; its values range between 0.0 and 5.0, and in most cases, results vary between 1.5 and 3.5, and rarely exceed 4.5 (Faurie et al., 2003). It was computed using the formula: $H'=-\sum\left(p_i\times\log_2 p_i\right)$, with $p_i=n_i/n$, where p_i is the proportion of individuals of species i (n_i) on the total number of individuals (n) of all species. Simpson's reciprocal index (SRI) was computed by SRI=$n\left(n-1\right)/\sum\left(n_i\left(n_i-1\right)\right)$. The ratio of observed value of Shannon's index to its maximum value gives the Pielou's evenness (E) index: $E=H'/H'_{max}$, with $H'_{max}=\log_2 S$, where S is the species richness. Values of E range between 0 and 1. When the value is getting closer to 1, it means that the plant community is equally distributed (Pielou, 1975).

2.3.2   Species richness estimation

The estimation of species richness of plants (S_{est}) was performed using the Estimate S program (Colwell and Elsensohn, 2014): (1) S_{est} that provided the expected number of plants for a given number of samples; (2) first $S_{(Jack1)}$ and second $S_{(Jack2)}$ order Jackknife's estimator: $S_{(Jack1)}=S+Q_1((m-1)/m)$, $S_{(Jack2)}=S+((Q_1(2m-3)/m)-(Q_2(m-2)^2/m(m-1)))$; (3) first $S_{(Chao1)}$ and second $S_{(Chao2)}$ order Chao's estimators: $S_{(Chao1)}=S+((n-1)/n\times(F_1(F_1-1))/(2(F_2+1)))$, $S_{(Chao2)}=S+((m-1)/m)(Q_1^2/2Q_2)$, where S is the observed species richness; m is the total number of samples; Q_1 and Q_2 are the frequency of unique (species that occur in only one sample) and duplicate (species that occur in only two samples), respectively; F_1 is the singletons; and F_2 is the doubletons. Values of species richness estimators were given as mean (±standard deviation)

following a 100-randomization runs.

2.3.3 Rarefaction and extrapolation

To make a comparison between the values of species richness between different communities observed in LSE, we established rarefaction and extrapolation curves for the entire area and for each LSE. This helped to evaluate the sampling effort and compared it with predicted richness. Using the observed data (the whole samples and samples at each LSE), the accumulation curve allowed to obtain an estimate of cumulative species richness. On the other hand, an extrapolation of species richness was made for a total number of 150 samples, i.e., 10 times higher than the reference sample for the whole area, and 30 times higher than the reference sample of each LSE.

2.3.4 Beta diversity

Using the software EstimateS (Colwell and Elsensohn, 2014), the analysis of species richness similarity between LSE was performed by computing several similarity indices. These include qualitative (Jaccard and Sørensen) and quantitative indices, namely raw and estimated Chao's Jaccard indices, raw and estimated Chao's Sørensen indices, Morisita-Horn index, and Bray-Curtis index (Chao et al., 2005).

2.4 Plant functional traits (PFT)

According to Lavorel et al. (2007) and Violle et al. (2007), PFT are observable characteristics of plants, widely used to represent the responses of vegetation to environmental conditions, and also the effects of vegetation on environment and climate, at scales from individuals to biomes. We attributed several PFT to each species. We determined these PFT based on previous studies (Negre, 1962; Quézel and Santa, 1962, 1963; Quézel, 1965; von Maydell, 1983; Jaouen, 1988; Ozenda, 1991; Audru et al., 1994; Jauffret, 2001; Tanji, 2005) and from the Tela-Botanica eflora database in North Africa (https://www.tela-botanica.org/flore/afrique-du-nord).

2.4.1 Raunkiaer's lifeform spectrum

Depending on the location and level of protection of buds or other renewing organs (seeds, tubers, and rhizomes) in relation to protection from unfavorable seasons (Al-Shaye et al., 2020), we categorized plant species of this study into five main groups, namely therophytes, geophytes, hemicryptophytes, chamaephytes, and phanerophytes, which are ligneous single-stem plants with perennating buds above the soil surface by at least 25 cm (Raunkiaer, 1934). These biological types were a combination of morphological characteristics resulting from the adaptations of species to environmental conditions (Sirven, 2020).

2.4.2 Dispersal spectrum

The dispersal spectrum is the frequency distribution of dispersal modes in a particular vegetation type, here in different LSE (Hughes et al., 1994). Depending on the agent involved in the dissemination of diaspores, we used a term to name the dispersal unit or mode of the plant (Weiher et al., 1999). van der Pijl (1982) distinguished five main categories that are anemochory, autochory, barochory, hydrochory, and zoochory. We made the determination of these types on the basis of literatures (Quézel and Santa, 1962, 1963; Jauffret, 2001; Ozenda, 2004; Bradai et al., 2015; Bouallala et al., 2020).

2.4.3 Morphological spectrum

We determined the morphological types based on Quézel and Santa (1962, 1963) and Ozenda (2004). Depending on the persistence of aerial vegetative part during unfavorable season, we classified the plants as perennial, biennial, or annual (Wang et al., 2018).

2.4.4 Grime's strategy

According to this model, species present in similar environments (i.e., stressed, disturbed, or productive environments) should have similar functional traits. The CSR (competition-stress-ruderality) model classified plants in respect to their responses to stress and disturbance into three main groups (Grime et al., 1988), which results in competitors (low stress and disturbance), stress-tolerators (high stress and low disturbance), and ruderals (low stress and high disturbance), and plants that have mixed and multiple responses to stress and disturbance types, i.e., CS, CR,

and SR for two responses, and CSR for three responses combined (Hall et al., 2020).

2.4.5   Noy-Meir's strategy

Based on plant photosynthetic activity during dry season, Noy-Meir (1973) classified plants into two categories (arido-passive and arido-active species) according to their drought adaptation strategy. The identification of Noy-Meir's strategy of adaptation in this study was based on the following works of Quézel and Santa (1962, 1963), Ozenda (2004), Jauffret (2001) and Bradai et al. (2015).

2.4.6   Chorological spectrum

According to Quézel (1978), the study area belongs to the Holarctic region, particularly to the Saharo-Arabian region (Saharan sub-region), and to the northern Sahara domain. The determination of chorological (or biogeographical) types of studied plants was referenced from the works of Quézel and Santa (1962, 1963) and Quézel (1965).

2.4.7   Analysis of plant ecological groups

Ecological group of each species was defined following Quézel (1965). Ecological groups retained in this study were psammophiles, gypsophiles, saxicoles, and ruderals.

2.4.8   Analysis of rarity/abundance status of flora

We determined rarity/abundance status of flora based on abundance appraisal retrieved from Quézel and Santa (1962, 1963). Each species was assigned to one of the following statuses: widespread (CCC), very common (CC), common (C), fairly common (AC), quite rare (AR), rare (R), and very rare (RR).

2.5   Statistical analysis

The data observed and/or computed at the level of sampling plots were exploited using free statistical software R (R Core Team, 2022). To compare beta diversity between and within LSE, we carried out nested Venn diagrams using the Venn package v.1.11 by displaying similarities of species richness intra and inter LSE. The variation in values of composition and taxonomic diversity parameters among LSE was tested using generalized linear model (GLM). Variables with count data (N and S) were fitted to GLM with Poisson distribution error and log link function, whereas the GLMs of other variables (VC, $N':S$, VC:N', VC:S, H', H'_{max}, E, SRI, SRI:S, and H':SRI) were implemented using Gaussian distribution and identity function. For each LSE, relationships between the above-mentioned composition and taxonomic diversity parameters were analyzed using Pearson's correlations. The resulting correlation matrices were visualized in an interactive plots using the R-corrplot package v.0.92. The relationships between these matrices were tested using two-tailed mantel test for a significance level of 0.05. Finally, because vegetation was investigated and characterized using multiple variables of different natures and aspects, a multiple factor analysis (MFA) was implemented to include all these studied variables into a single analysis. The MFA studied multiple tables of plant characteristics for different LSE, then highlighted patterns and distinguished between LSE based on plant variables. In our case, each table (i.e., different measured parameters, such as PFT) gathered a group of individuals (i.e., different plant traits). We implemented the MFA based on ten plant variables, i.e., lifeforms (chamaephytes, hemicryptophytes, and phanerophytes), morphological types (annuals and perennials), dispersal types (anemochore, barochore, and zoochore), Noy-Meir's strategy (arido-active and arido-passive), Grime's strategy (CSR, CS, SR, and S), chorological categories (NA, M-SA, Sah, and SA), rarity/abundance status (CCC, CC, C, AC, AR, R, and RR), density parameters (VC, N', VC:N', VC:S, and $N':S$), diversity indices (S, H', H'_{max}, E, SRI, and SRI:S), and the characteristic and common species of all LSE (*A. articulata*, *Centropodia forsskaolii* (Vahl) Cope, *Mecomischus halimifolius* (Munby) Hochr., and *T. microphylla*).

3   Results

3.1   Flora composition and abundance

Overall, 19 plant species were identified, belonging to 18 genera and 13 families (Table 1). The

Table 1 Taxonomic list, density, and occurrence frequency of plant species sampled at desert pavements under different levels of sand encroachment in the Sahara Desert of Algeria

Family	Species	Level of sand encroachment (LSE)			
		Low (LLSE)	Moderate (MLSE)	High (HLSE)	Overall
Amaranthaceae	*Anabasis articulata* (Forssk.) Moq.	29.8±5.1 [149] (100%)	10.0±9.5 [50] (100%)	5.0±2.5 [25] (100%)	14.9±12.6 [224] (100%)
Apiaceae	*Deverra scoparia* subsp. *scoparia* Coss. & Durieu	-	-	0.2±0.4 [1] (20%)	0.1±0.3 [1] (7%)
Asteraceae	*Mecomischus halimifolius* (Munby) Hochr.	1.0±1.4 [5] (40%)	1.2±1.1 [6] (60%)	2.6±2.1 [13] (80%)	1.6±1.6 [24] (60%)
Asteraceae	*Pulicaria undulata* subsp. *undulata* (L.) C.A. Mey.	0.6±0.9 [3] (40%)	0.6±0.5 [3] (60%)	-	0.4±0.6 [6] (33%)
Asteraceae	*Rhanterium suaveolens* Desf.	-	0.2±0.4 [1] (20%)	0.6±0.9 [3] (40%)	0.3±0.6 [4] (20%)
Boraginaceae	*Moltkiopsis ciliata* (Forssk.) I.M. Johnst.	2.2±3.3 [11] (60%)	0.6±0.5 [3] (60%)	-	0.9±2.1 [14] (40%)
Brassicaceae	*Moricandia nitens* (Viv.) E.A. Durand & Barratte	0.2±0.4 [1] (20%)	2.8±2.6 [14] (60%)	-	1.0±1.9 [15] (27%)
Caryophylla-ceae	*Polycarpaea repens* (Forssk.) Asch. & Schweinf.	2.8±2.6 [14] (60%)	1.6±2.3 [8] (40%)	-	1.5±2.2 [22] (33%)
Cistaceae	*Helianthemum lippii* (L.) Dum. Cours.	-	0.2±0.4 [1] (20%)	0.6±0.9 [3] (40%)	0.3±0.6 [4] (20%)
Ephedraceae	*Ephedra alata* subsp. *alenda* (Stapf) Trab.	-	-	1.6±2.1 [8] (60%)	0.5±1.4 [8] (20%)
Euphorbia-ceae	*Euphorbia guyoniana* Boiss. & Reut.	-	2.0±1.0 [10] (100%)	-	0.7±1.1 [10] (33%)
Fabaceae	*Calobota saharae* (C&D) Boatwr. & van Wyk	-	-	14.2±5.2 [71] (100%)	4.7±7.5 [71] (33%)
Fabaceae	*Retama raetam* (Forssk.) Webb	-	0.2±0.4 [1] (20%)	-	0.1±0.3 [1] (7%)
Poaceae	*Centropodia forsskaolii* (Vahl) Cope	1.4±3.1 [7] (20%)	0.8±1.3 [4] (40%)	2.0±3.5 [10] (40%)	1.4±2.6 [21] (33%)
Poaceae	*Stipagrostis acutiflora* (Trin. & Rupr.) De Winter	0.4±0.9 [2] (20%)	-	-	0.1±0.5 [2] (7%)
Poaceae	*Stipagrostis pungens* (Desf.) De Winter	-	-	0.2±0.4 [1] (20%)	0.1±0.3 [1] (7%)
Scrophularia-ceae	*Kickxia aegyptiaca* (L.) Nábelek	2.0±2.9 [10] (60%)	0.2±0.4 [1] (20%)	-	0.7±1.8 [11] (27%)
Scrophularia-ceae	*Scrophularia syriaca* Benth. A. DC.	2.4±1.3 [12] (100%)	3.6±1.7 [18] (100%)	-	2.0±1.9 [30] (67%)
Thymelaea-ceae	*Thymelaea microphylla* Coss. & Durieu ex Meisn.	2.0±2.1 [10] (60%)	19.4±11.3 [97] (100%)	3.0±1.6 [15] (100%)	8.1±10.3 [122] (87%)

Note: means±SD, with the total of number of individuals displayed between square brackets. Species occurrence frequency (%) in samples are shown in round brackets. -, no data.

variation in floristic composition and abundance was notable and dependent on LSE. The plant species that recorded the highest values density, number of individuals, and occurrence frequency was *A. articulata*. While the lowest values were recorded in the following species: *Deverra scoparia* subsp. *scoparia* Coss. & Durieu, *Retama raetam* (Forssk.) Webb, and *Stipagrostis pungens* (Desf.) De Winter. Depending on LSE, *A. articulata* predominated in LLSE, while its highest values were recorded in MLSE. *C. saharae* was dominant in HLSE.

3.2　Importance of botanical families for different LSE

For different LSE, a variation in the distribution of different families was reported (Table 2). Poaceae and Asteraceae were the most represented families in the study area, followed by Amaranthaceae and Thymelaeaceae, and then Apiaceae. Depending on the type sampled LSE, the variation was notable. In LLSE, the families that recorded the highest values of relative frequencies of species richness were Asteraceae, Poaceae, and Scrophulariaceae. But the relative frequencies of abundances showed that the highest value was detained by Amaranthaceae. In MLSE, the highest value of species richness was recorded in Asteraceae, but the highest value of abundance-based relative frequency was reported in Thymelaeaceae. In HLSE, Asteraceae and Poaceae had the highest values of species composition, whereas Fabaceae was dominant in terms of number of individuals.

Table 2　Species richness (S) and density (N') with relative frequencies (RF) of plant families at desert pavements under different levels of sand encroachment in the Sahara Desert of Algeria

Family	No. of genus	Low (LLSE)		Moderate (MLSE)		High (HLSE)		Overall	
		S (RF)	N' (RF)	S (RF)	N' (RF)	S (RF)	N' (RF)	S (RF)	N' (RF)
Amaranthaceae	1	1 (9.1%)	149 (66.5%)	1 (7.1%)	50 (23.0%)	1 (10.0%)	25 (16.7%)	1 (5.3%)	224 (37.9%)
Apiaceae	1	-	-	-	-	1 (10.0%)	1 (0.7%)	1 (5.3%)	1 (0.2%)
Asteraceae	3	2 (18.2%)	8 (3.6%)	3 (21.4%)	10 (4.6%)	2 (20.0%)	16 (10.7%)	3 (15.7%)	34 (5.8%)
Boraginaceae	1	1 (9.1%)	11 (4.9%)	1 (7.1%)	3 (1.4%)	-	-	1 (5.3%)	14 (2.4%)
Brassicaceae	1	1 (9.1%)	1 (0.4%)	1 (7.1%)	14 (6.5%)	-	-	1 (5.3%)	15 (2.5%)
Caryophyllaceae	1	1 (9.1%)	14 (6.3%)	1 (7.1%)	8 (3.7%)	-	-	1 (5.3%)	22 (3.7%)
Cistaceae	1	-	-	1 (7.1%)	1 (0.5%)	1 (10.0%)	3 (2.0%)	1 (5.3%)	4 (0.7%)
Ephedraceae	1	-	-	-	-	1 (10.0%)	8 (5.3%)	1 (5.3%)	8 (1.4%)
Euphorbiaceae	1	-	-	1 (7.1%)	10 (4.6%)	-	-	1 (5.3%)	10 (1.7%)
Fabaceae	2	-	-	1 (7.1%)	1 (0.5%)	1 (10.0%)	71 (47.3%)	2 (10.4%)	72 (12.2%)
Poaceae	2	2 (18.2%)	9 (4.0%)	1 (7.1%)	4 (1.8%)	2 (20.0%)	11 (7.3%)	3 (15.7%)	24 (4.1%)
Scrophulariaceae	2	2 (18.2%)	22 (9.8%)	2 (14.3%)	19 (8.8%)	-	-	2 (10.5%)	41 (6.9%)
Thymelaeaceae	1	1 (9.1%)	10 (4.5%)	1 (7.1%)	97 (44.7%)	1 (10.0%)	15 (10.0%)	1 (5.3%)	122 (20.6%)
Total	18	11 (100.0%)	224 (100.0%)	14 (100.0%)	217 (100.0%)	10 (100.0%)	150 (100.0%)	19 (100.0%)	591 (100.0%)

Note: -, no data.

3.3　Species richness partitioning

Overall, the sampled LSE studied encompassed 19 species, of which 14 species colonized MLSE, whereas LLSE and HLSE had 10 and 11 species, respectively (Fig. 2). The species *A. articulata*, *C. forsskaolii*, *M. halimifolius* and *T. microphylla* turn out to be common, even omnipresent among the three LSE. Other species were exclusive, the case of *S. acutiflora* in LLSE, *Euphorbia guyoniana* Boiss. & Reut. and *R. raetam* in MLSE, and *D. scoparia*, *Ephedra alata* ssp. *alenda*, *C. saharae* and *S. pungens* in HLSE. Six species were exclusively shared between LLSE and MLSE (*Pulicaria undulata* subsp. *undulata* (L.) C.A. Mey., *Moricandia nitens* (Viv.) E.A. Durand & Barratte, *Polycarpaea repens* (Forssk.) Asch. & Schweinf., *Moltkiopsis ciliate* (Forssk.) I.M. Johnst., *Scrophularia syriaca* Benth. in A. DC., and *Kickxia aegyptiaca* (L.) Nábelek). And 2 species were exclusive in MLSE and HLSE (*Helianthemum lippii* (L.) Dum. Cours. and *Rhanterium suaveolens* Desf.). Finally, no exclusive species occurred between LLSE and HLSE. It is noteworthy to mention that 4 common species above reported and shared species exclusively among LSE were also the common species among sampling sites within each LSE.
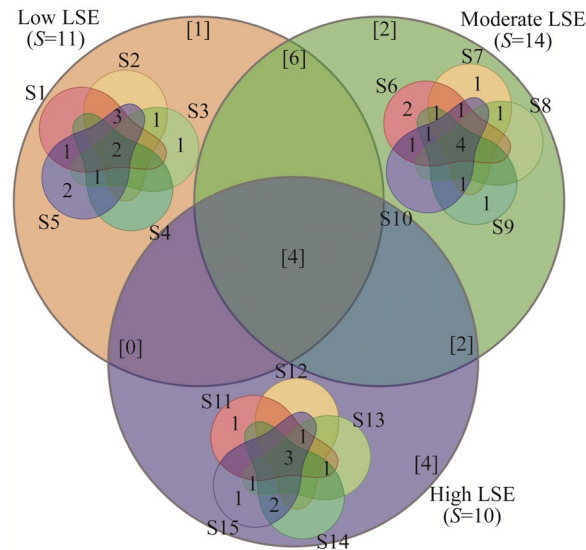
Fig. 2 Partitioning of plant species richness (*S*) recorded at desert pavements in the Sahara Desert of Algeria using nested Venn diagrams. Values of *S* reported between round brackets represent the total number of species recorded at each level of sand encroachment. Number of species shared exclusively between habitats with different levels of sand encroachment (LSE) and sampling sites are designated between square brackets and within the five-set diagrams, respectively.

3.4   Species richness estimation

The estimation of species richness through the nonparametric estimators S_{Chao1}, S_{Chao2}, S_{Jack1}, and S_{Jack2} revealed variable predictions from one estimator to another (Fig. 3). In the study area as a whole, the application of S_{Chao1} and S_{Chao2} estimators allowed to predict an increase in species richness of 7% (inventory completeness=93%) for S_{Chao1} and 23% (completeness=77%) for S_{Chao2} to reach 20.5 (±2.6) and 24.6 (±6.8) species, respectively. This increase was expected to be 16% (completeness=84%) by S_{Jack1} (S_{Jack1}=22.7 (±1.6)) and 27% (inventory completeness=73%) for S_{Jack2} with S_{Jack2}=26.2 (±0.0) species. With respect to LSE, by applying Chao1 and Chao2 in sampled LSE with LLSE (*S*=11.0 species), the predicted increases were 0% and 7% with 100% and 93% of completeness, respectively, that is equivalent to 11.0 and 11.8 species; whereas it was 18% (S_{Jack1}) and 23% (S_{Jack2}) corresponding to 13.4 and 14.0 species. In MLSE, 14.0 observed species would experience an increase by 30% with S_{Chao1} (S_{Chao1}=20.0 species, completeness of 70%) and 10% with S_{Chao2} with 15.6 species (completeness of 90%). As for S_{Jack1} and S_{Jack2}, the increase was expected to be 19% (81% completeness) and 25% (75% completeness), respectively, corresponding to 17.2 and 18.7 species. Finally, in the case of HLSE, the increase by S_{Chao1} was 9%, corresponding to 11.0 species, 2% (S_{Chao2}=10.2 species), 14% (S_{Jack1}=11.6 species) and 13% (S_{Jack2}=11.5 species).

3.5   Species richness interpolation

Species extrapolation curves revealed that the estimated values of specific richness (S_{est}) increased slowly with the increase in the number of samples (Fig. 4). At 150 samples, i.e., 10 times more than the reference sample (*m*=15 with *S*=19 and *n*=591), and independently of LSE, the richness would increase by 29.4% for a number of individuals of 5910, reaching 24.6 (±5.9) species. On the other hand, with LSE, at 150 samples (30 times more the reference sample) an increase of 16.4% corresponding to 12.8 (±2.7) species for a total number of individuals of 6720 was expected in the case of LLSE (S_{obs}=11, *n*=224). With MLSE (S_{obs}=14, *n*=217), this increase would be 22.9% equivalent to 17.2 (±4.1) species for a total of 6510 individuals. Finally, the predicted richness in the case of HLSE was 10.5 (±1.1) species for 4500 individuals, which corresponded to an increase of 5.3% (S_{obs}=10, *n*=150). In all cases, the plateau in curves was quickly reached even before reaching the 20th sample and a little more, regardless of LSE (Fig. 4).
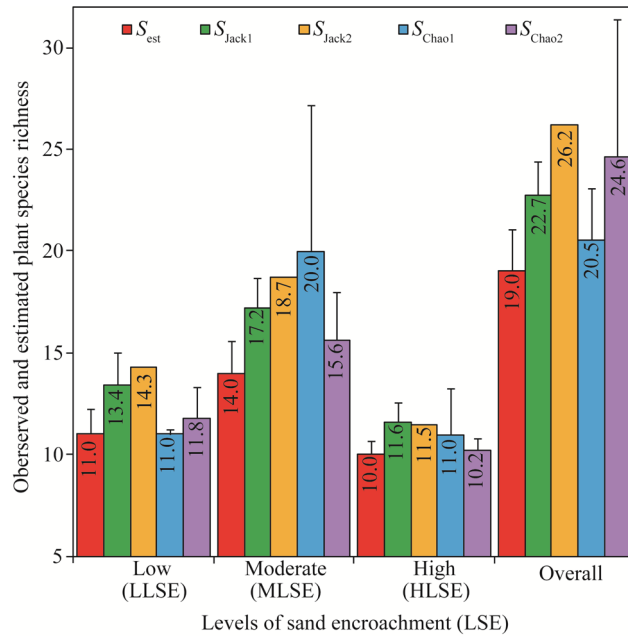
Fig. 3 Observed and estimated plant species richness at desert pavements under different levels of sand encroachment in the Sahara Desert of Algeria. Species richness was estimated using first- and second-order Jackknife's (S_{Jack1} and S_{Jack2}) and Chao (S_{Chao1} and S_{Chao2}) estimators. Vertical bars represent standard deviations. S_{est}, estimated species richness.
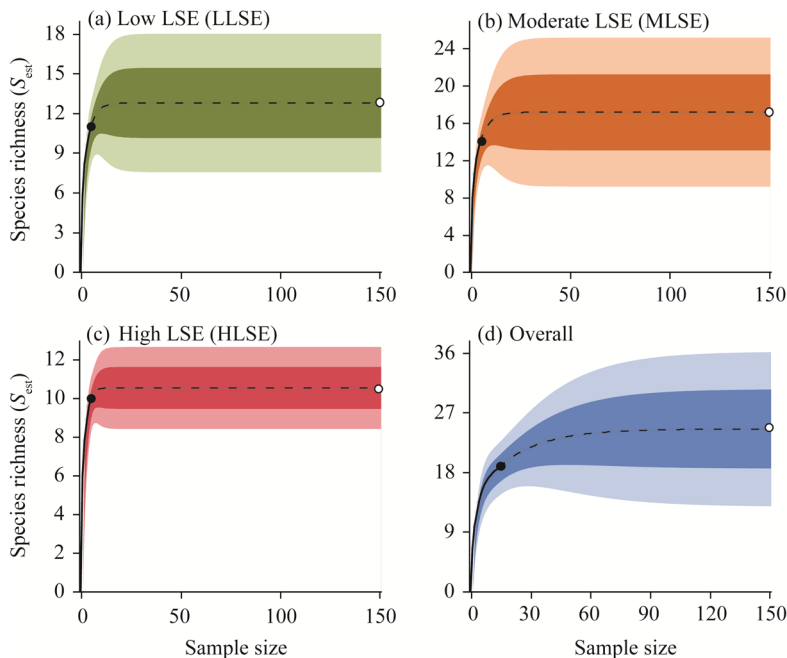

Fig. 4 Sample-based rarefaction (solid line) and extrapolation (dashed line) curves of estimated plant species richness at desert pavements under different levels of sand encroachmentin (LSE) in the Sahara Desert of Algeria. Black solid circles indicate species richness estimated based on reference samples, whereas white solid circles refer to extrapolation to 150 samples. Dark colored areas indicate standard deviations, and light colored areas represent lower and upper bounds of 95% confidence intervals for the estimated values. (a), low LSE (LLSE); (b), moderate LSE (MLSE); (c), high LSE (HLSE); (d), overall.

3.6 Plant diversity patterns

The variation of different diversity parameters in sandy desert pavements of the Algeria (Fig. 5)

revealed low values regardless of LSE. Indeed, the vegetation cover per sampling plot (100 m²) varied between 14% and 16% with the increase in intensity of LSE. Plant density scored 44.80 (±5.17) individuals in LLSE, while it averaged 43.40 (±19.17) and 30.00 (±8.22) individuals in MLSE and HLSE, respectively. Plant diversity parameters (H', E, and SRI) differed between different LSE. Under MLSE, assemble of plants recorded slightly higher values (S=8.00 (±1.87) species, H'=2.24 (±0.45), E=0.76 (±0.14), SRI=4.34 (±2.07)) compared with HLSE (S=6.00 (±1.41) species, H'=2.04 (±0.16), E=0.81 (±0.09), SRI=3.62 (±0.50)) and LLSE (S=5.80 (±2.17) species, H'=1.51 (±0.75), E=0.59 (+0.20), SRI=2.35 (±1.06)). Apart from VC:N' ratio that displayed higher value in HLSE, VC:S and N':S ratios were higher in LLSE. Finally, SRI:S and
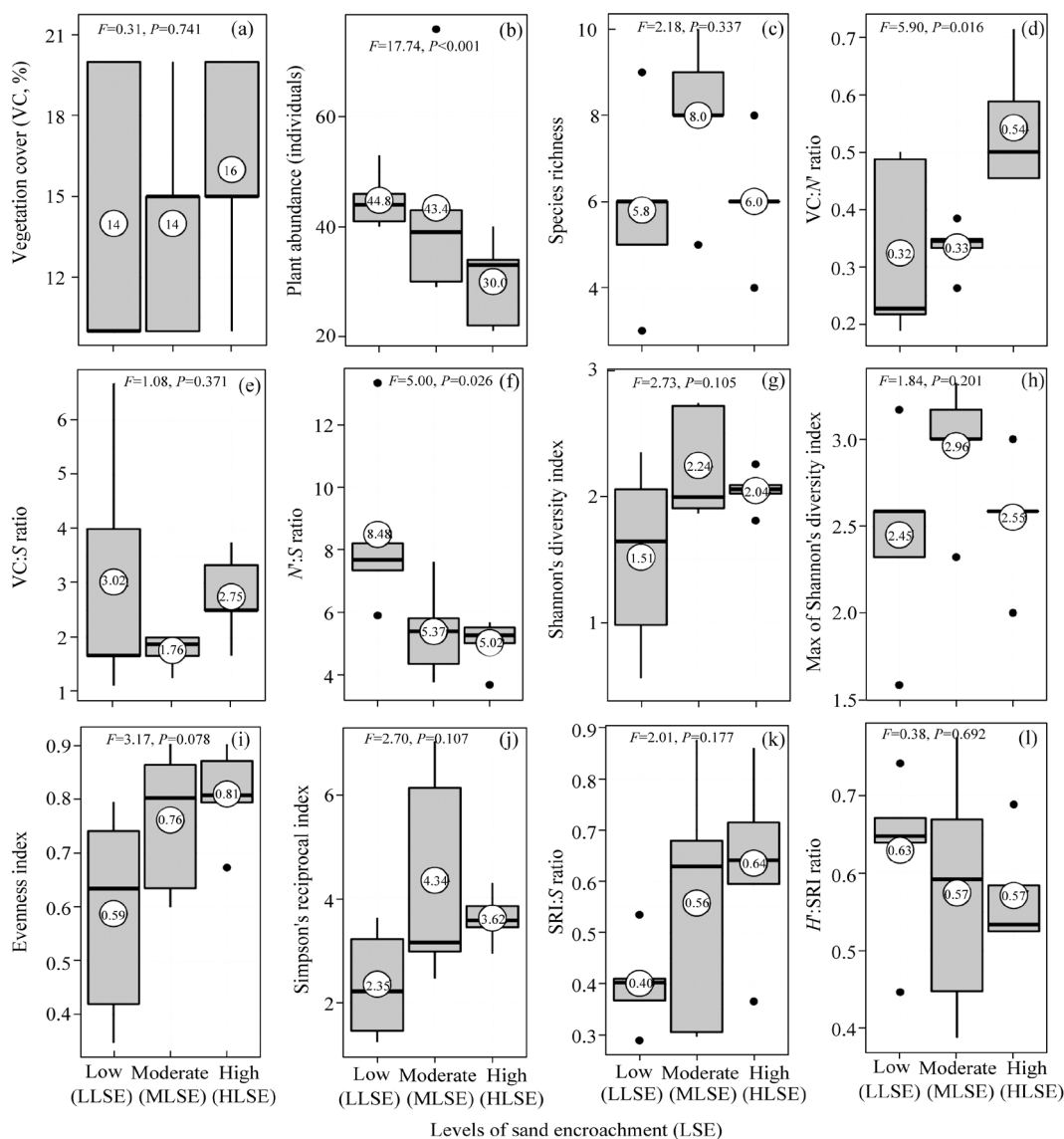

Fig. 5 Variation of diversity parameters at desert pavements under different levels of sand encroachment in the Sahara Desert of Algeria. Boxes indicate the IQR (interquartile range, 75th to 25th of the data). The median value is shown as a line within the box. White circle is shown as mean. Outlier is shown as black circle. Whiskers extend to the most extreme value within 1.5×IQR. (a), vegetation cover (VC); (b), plant abundance; (c), species richness (S); (d), individual cover (VC:N' ratio), N', density; (e), species cover (VC:S ratio); (f), species abundance (N':S ratio); (g), Shannon's diversity index; (h), maximum Shannon's diversity index (H'max); (i), Evenness index; (j), Simpson's reciprocal index (SRI); (j), SRI:S ratio; (k), H':SRI ratio. The abbreviataions are the same in the following figures and tables.

H':SRI ratios varied slightly between LSE. GLMs testing the statistical variations of above-mentioned parameters among the studied LSE demonstrated that significant differences were observed in plant density ($F=17.70$, $P<0.001$), VC:N' ratio ($F=5.90$, $P=0.016$), and N':S ratio ($F=5.00$, $P=0.026$).

3.7   Analysis of similarity

With all the indices of similarity, the greatest affinity was recorded between communities linked to LLSE and MLSE, explained by the values of 66.7% and 80.0% for indices of Jaccard and Sorenson, 93.2% (raw Chao-Jaccard index), 97.2% (estimated Chao-Jaccard index), 96.5% (raw Chao-Sorenson index), 98.6% (estimated Chao-Sorenson index), 50.3% (Morisita-Horn index) and 44.0% (Bray-Curtis index) (Table 3); otherwise it rarely exceeded 50.0% between LLSE and HLSE or between MLSE and HLSE.

Table 3   Qualitative and abundance-based similarity scores between plant communities at desert pavements under different levels of sand encroachment in the Sahara Desert of Algeria

Similarity estimator	Levels of sand encroachment (LSE)		
	Low (LLSE) (S=11) Moderate (MLSE) (S=14)	Low (LLSE) (S=11) High (HLSE) (S=10)	Moderate (MLSE) (S=14) High (HLSE) (S=10)
Shared species observed	10.0	4.0	6.0
Estimated Chao-shared	10.7	4.0	7.6
Classic Jaccard index (%)	66.7	23.5	33.3
Classic Sørensen index (%)	80.0	38.1	50.0
Raw Chao-Jaccard index (%)	93.2	37.2	39.4
Estimated Chao-Jaccard index (%)	97.2	37.2	42.3
Raw Chao-Sørensen index (%)	96.5	54.2	56.5
Estimated Chao-Sørensen index (%)	98.6	54.2	59.4
Morisita-Horn index (%)	50.3	32.5	31.8
Bray-Curtis index (%)	44.0	25.1	28.3

3.8   Interrelationship between vegetation diversity at different LSE

The relationships between abundance, cover, and diversity parameters of vegetation at different LSE in the study area revealed many significant ($P<0.05$) and positive correlations (Fig. 6). These correlations dominated under LLSE affecting the following pairs of parameters: VC–VC:N' ($P<0.001$), VC–VC:S ($P=0.033$), VC–H' ($P=0.027$), VC–E ($P=0.015$), N'–S ($P=0.011$), N'–H' ($P=0.031$), N–H'_{max} ($P=0.042$), N'–SRI ($P=0.020$), S–N':S ($P=0.041$), S–H' ($P=0.028$), S–H'_{max} ($P=0.003$), S–SRI ($P=0.047$), N':S–VC:S ($P=0.014$), N':S–H'_{max} ($P=0.008$), VC:N'–VC:S ($P=0.028$), VC:N'–H' ($P=0.014$), VC:N'–E ($P=0.011$), VC:N'–SRI ($P=0.034$), VC:S–H' ($P=0.016$), CV:S–H'_{max} ($P=0.017$), CV:S–E ($P=0.028$), H'–H'_{max} ($P=0.020$), H'–E ($P=0.002$), H'–SRI ($P=0.004$) and finally E–SRI ($P=0.014$).

Under MLSE, the significant correlations were observed between the pairs VC–N ($P=0.017$), S–H'_{max} ($P=0.000$), H'–SRI ($P=0.008$), E–SRI:S ($P=0.003$), whereas in HLSE, the significant correlations included S–H'_{max} ($P=0.001$), S–E ($P=0.029$), S–SRI:S ($P=0.008$), VC:N'–VC:S ($P=0.035$), H'_{max}–SRI:S ($P=0.017$), and E–SRI:S ($P=0.004$). According to two-tail Mantel tests, different correlation matrices (Fig. 6) were positively associated, with a stronger correlation between MLSE–HLSE ($P<0.001$) compared with LLSE–MLSE ($P=0.035$) and LLSE–HLSE ($P=0.016$).

3.9   Plant functional diversity

3.9.1   Lifeform

According to species- and abundance-based spectra (Table 4; Fig. 7), chamaephytes predominated, while phenerophytes and therophytes were weakly represented. This finding is valid for both the
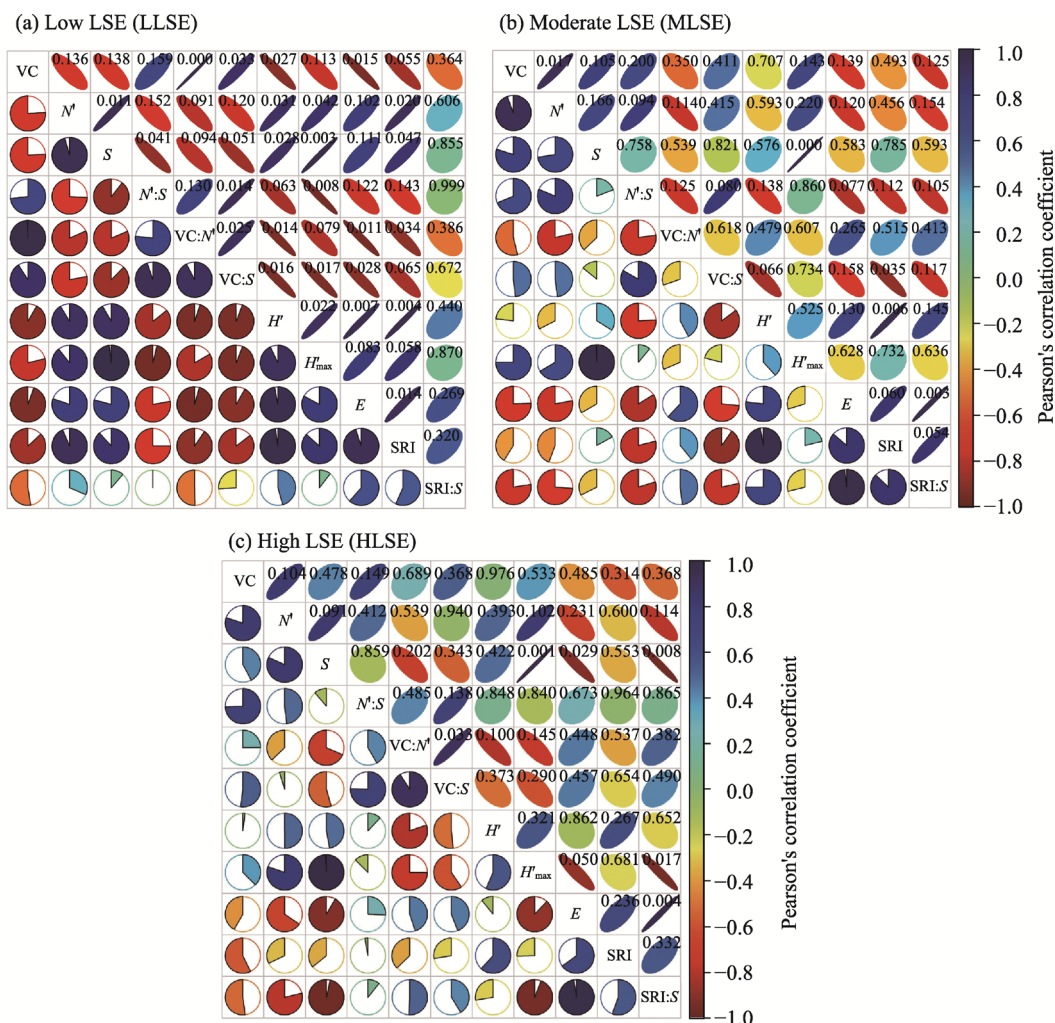
Fig. 6 Correlation matrices exposing correlations between plant characteristics (vegetation cover, plant abundance, and diversity parameters) at desert pavements under different levels of sand encroachment (LSE) in the Sahara Desert of Algeria. (a), low LSE (LLSE); (b), moderate LSE (MLSE); (c), high LSE (HLSE).

whole study area and LSE when considered separately. Hemicryptophytes were moderately represented in all LSE.

3.9.2   Morphological type

Regardless of the type of spectra (abundance- or species richness-based), with the exception of HLSE, where annuals were absent, perennials predominated in LLSE and MLSE as well as in the study area when considered all LSE pooled (Fig. 7).

3.9.3   Dispersal type

For the whole study area and at each LSE, the predominance of anemochores was observed in plant dissemination types (Fig. 7). This type of plants with wind-borne seeds was also prominent in the density spectrum, but only in LLSE. Barochores co-dominated in second place in the study area, but it predominated in MLSE and HLSE. Zoochores were either absent or poorly represented, regardless of LSE.

3.9.4   Noy-Meir's strategy

The spectra of species richness and density of Noy-Meir's strategy showed a very clear dominance of arido-active plants compared with arido-passive species for all LSE and the whole study area (Fig. 7).

Table 4　Lfeform, morphological (morp) type, dispersal type, Noy-Meir's category, Grime's strategy, phytogeographic (phyt) type, rarity status, and ecology of plant species at desert pavements under different levels of sand encroachment in the Sahara Desert of Algeria

Plant species	Lifeform	Morp type	Dispersal type	Noy-Meir's type	Grime's strategy	Phyt type	Rarity status	Ecology
Anabasis articulata	Cham	Perennial	Anemo	Arido-active	CS	SA	C	Psa, Sax
Centropodia forsskaolii	Hemi	Perennial	Anemo	Arido-passive	CS	SA	CC	Psa
Ephedra alata	Phan	Perennial	Anemo	Arido-active	Str	SA	CC	Psa
Euphorbia guyoniana	Hemi	Perennial	Baro	Arido-passive	Str	S′	CC	Psa
Calobota saharae	Cham	Perennial	Baro	Arido-active	CS	S′	AR	Psa
Helianthemum lippii	Cham	Perennial	Anemo	Arido-passive	CSR	M-SA	CCC	Sax, gyps-sax
Kickxia aegyptiaca	Cham	Perennial	Anemo	Arido-active	CS	M-SA	C	Sax, gyps-sax
Mecomischus halimifolius	Cham	Perennial	Anemo	Arido-active	CS	End	RR	Psa
Moltkiopsis ciliata	Cham	Perennial	Anemo	Arido-active	CS	SA	C	Psa
Moricandia nitens	Cham	Perennial	Baro	Arido-passive	Str	S′	AR	Rud, gyps
Deverra scoparia	Cham	Perennial	Zoo	Arido-active	Str	M-SA	C	Sax
Polycarpaea repens	Ther	Annual	Anemo	Arido-passive	SR	SA	RR	Psa
Pulicaria undulata	Cham	Perennial	Anemo	Arido-active	Str	SA	AC	Gypv
Retama raetam	Phan	Perennial	Baro	Arido-active	Str	M-SA	C	Psa
Rhanterium suaveolens	Cham	Perennial	Zoo	Arido-active	CS	SA	R	Sax, gyps-sax
Scrophularia syriaca	Cham	Perennial	Baro	Arido-passive	Str	M-SA	CC	Psa
Stipagrostis acutiflora	Hemi	Perennial	Anemo	Arido-active	CS	SA	R	Psa
Stipagrostis pungens	Hemi	Perennial	Anemo	Arido-active	CS	SA	CC	Psa
Thymelaea microphylla	Cham	Perennial	Baro	Arido-active	Str	M-SA	CC	Sax, gyps-sax

Note: Cham, chamaephyte; Hemi, hemicryptophyte; Phan, phanerophytes; Ther, therophytes; Anemo, anemochore; Baro, barochore; CSR, competition-stress-ruderality; Str, stress-tolerant; CS, competition-stress; SR, stress-ruderality; End, endemic; M-SA, Mediterranean-Saharo-Arabian; S′, Saharan; SA, Saharo-Arabian; CCC, widespread; CC, very common; C, common; AC, fairly common; AR, quite rare; R, rare; RR, very rare; Gyps, gypsophyte; Gypv, gypsovag; Psa, psammophyte; Rud, ruderal; Sax, saxicolous. The abbreavitaions are the same in the following figures and tables.

3.9.5　Grime's strategy

Species-based spectrum of Grime's strategy showed a predominance of CS strategy (competitive and stress-tolerant) throughout the study area and in different LSE (Fig. 7). The same was true for the density-based spectrum, but except in MLSE, where stress tolerant plants predominated. Plants with CSR and SR strategies were very poorly represented both in terms of species richness and abundance and both at the scale of LSE, and even at the whole study area.

3.9.6　Chorological type

Based on species richness spectrum (Fig. 7), the Saharo-Arabian category was well represented in the whole study area and different LSE. In terms of abundance, the chorological type 'Saharo-Arabian' was exclusively dominating in LLSE and the study area. In MLSE, Mediterranean-Saharo-Arabian plants predominated, while Saharan plants colonized HLSE. Finally, the endemic plants to Algerian-Moroccan Sahara were very weakly represented in all sandy gravels both in terms of plant richness and density.

3.10　**Plant ecological category and rarity status**

Regardless of LSE, a predominance in relative frequency of species richness of psammophytes (S=48.0%, N'=26.2%–65.3%) was recorded. This was accompanied by a weak representation of gypsovags and ruderals (Table 5). For the rarity status in the flora of Algeria, based of species relative frequency, there was an absence of plants of CCC in LLSE. CC and C plant species were well represented (27.3% for each), accompanied by a significant percentage of RR species
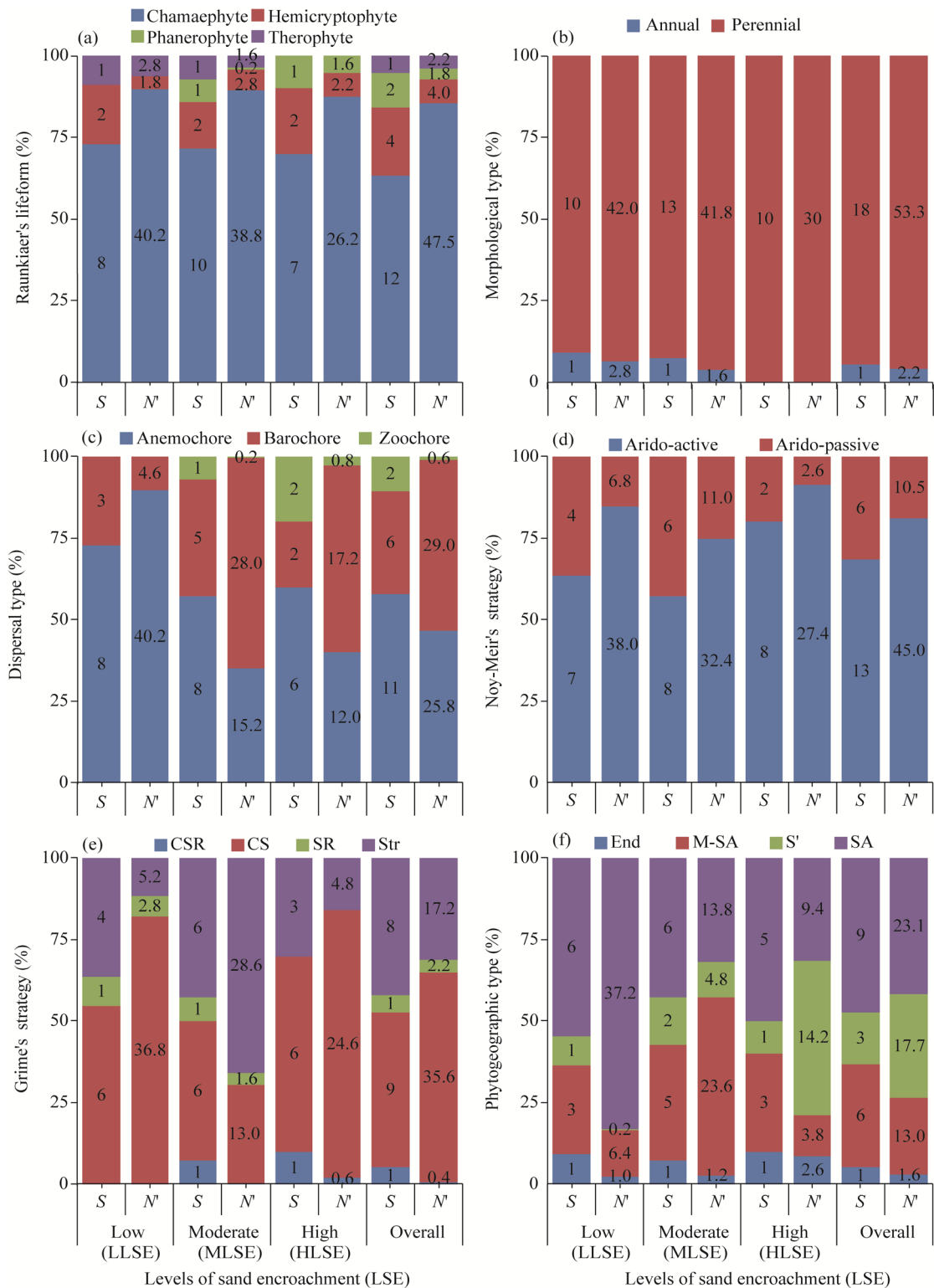
Fig. 7 Species- and abundance-based biological spectra of plant functional traits (Raunkiaer's lifeform (a), morphological type (b), dispersal type (c), Noy-Meir's strategy (d), Grime's strategy (e), and phytogeographic type (f)) characterizing the vegetation associated to desert pavements under different levels sand encroachment in the Sahara Desert of Algeria. S, species richness; N', density.

(S=18.2%). Abundance-based frequencies showed a predominance of C species (N'=75.9%). The species richness of the category CC and C predominated in MLSE with S=28.6%. Based on abundance, CC species predominated with 59.4%. In HLSE, species richness of CC type was well represented (S=40.0%), while species with AC status was absent. In terms of abundance, AR predominated with N'=47.3%. In the whole study area, CC status predominated in terms of species richness (S=31.6%), while it was the category of C that predominated in terms of abundance (N'=42.5%).

Table 5 Species richness (S) and density (N') with relative frequencies (RF) of ecological groups and rarity-abundance status for plants at desert pavements under different sand encroachment levels in the Sahara Desert of Algeria

Plant status	Levels of sand encroachment (LSE)							
	Low (LLSE)		Moderate (MLSE)		High (HLSE)		Overall	
	S (RF)	N' (RF)	S (RF)	N' (RF)	S (RF)	N' (RF)	S (RF)	N' (RF)
Ecological category								
Psammophyte	12 (48.0%)	200 (50.8%)	12 (48.0%)	100 (26.2%)	12 (48.0%)	128 (65.3%)	12 (48.0%)	428 (44.1%)
Saxicolous	6 (24.0%)	169 (42.9%)	6 (24.0%)	150 (39.4%)	6 (24.0%)	47 (24.0%)	6 (24.0%)	366 (37.7%)
Gypsophyte	5 (20.0%)	21 (5.3%)	5 (20.0%)	114 (29.9%)	5 (20.0%)	21 (10.7%)	5 (20.0%)	156 (16.1%)
Gypsovag	1 (4.0%)	3 (0.8%)	1 (4.0%)	3 (0.8%)	1 (4.0%)	-	1 (4.0%)	6 (0.6%)
Ruderal	1 (4.0%)	1 (0.3%)	1 (4.0%)	14 (3.7%)	1 (4.0%)	-	1 (4.0%)	15 (1.5%)
Rarity/abundance status								
CCC	-	-	1 (7.1%)	1 (0.5%)	1 (10.0%)	3 (2.0%)	1 (5.3%)	4 (0.7%)
CC	3 (27.3%)	29 (12.9%)	4 (28.6%)	129 (59.4%)	4 (40.0%)	34 (22.7%)	6 (31.6%)	192 (32.5%)
C	3 (27.3%)	170 (75.9%)	4 (28.6%)	55 (25.3%)	2 (20.0%)	26 (17.3%)	5 (26.3%)	251 (42.5%)
AC	1 (9.1%)	3 (1.3%)	1 (7.1%)	3 (1.4%)	-	-	1 (5.3%)	6 (1.0%)
AR	1 (9.1%)	1 (0.4%)	1 (7.1%)	14 (6.5%)	1 (10.0%)	71 (47.3%)	2 (10.5%)	86 (14.6%)
R	1 (9.1%)	2 (0.9%)	1 (7.1%)	1 (0.5%)	1 (10.0%)	3 (2.0%)	2 (10.5%)	6 (1.0%)
RR	2 (18.2%)	19 (8.5%)	2 (14.3%)	14 (6.5%)	1 (10.0%)	13 (8.7%)	2 (10.5%)	46 (7.8%)
Total	11 (100.0%)	224 (100.0%)	14 (100.0%)	217 (100.0%)	10 (100.0%)	150 (100.0%)	19 (100.0%)	591 (100.0%)

Note: -, no data.

3.11 Vegetation pattern associated to desert pavements under SLA

MFA result confirmed totaled 100.00% of explained variance, with 62.89% on the first dimension and 37.11% on the second dimension (Fig. 8). This analysis highlighted the associations between the measured traits and attributed characteristics of vegetation according to LSE. We distinguished the latter from each other according to the variables of vegetation. According to first axis of MFA, we distinguished desert pavements with HLSE from the other two LSE by morphological type, phytogeographic type, rarity status, density parameter, lifeform, and Noy-Meir's strategy. While the second axis differentiated between MLSE and LLSE according to Grime's strategy, diversity score, dispersal type, and common species. The plant communities encountered in LLSE and MLSE converged mainly by similarities in morphological type and Noy-Meir's strategy, and then by rarity status, density parameter, and lifeform. Plant community of desert pavement under HLSE presented similar schemes with MLSE following the effects of plant diversity parameter and dispersal type, while the density of common species between these LSE contributed to their segregation apart. The converging variables between communities of LLSE and HLSE were scores of diversity parameters and common species densities. The MFA indicated that with the increase in LSE, i.e., along the gradient from LLSE to HLSE, plant communities strike sharp changes in plant variables including decrease in plant densities with

changes in chorological categorie, rarity status, lifeform, morphological type, and Noy-Meir's strategy. Indeed, the variants and sub-traits of these variables were significantly related to each other. Considering the PFT patterns of plant communities shown in Figure 7, chamaephyte, perennial, plant density (N'), anemochorous, arido-active, and CC species were positively correlated (Fig. S1).
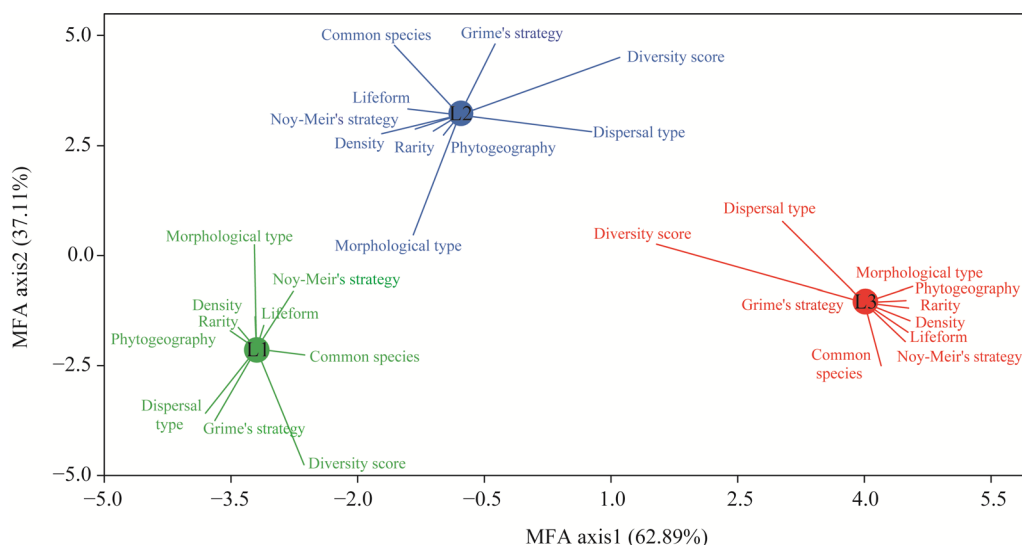

Fig. 8 Vegetation pattern associated to desert pavements under different levels of sand encroachment in the Sahara Desert of Algeria. L1, low LSE; L2, moderate LSE; L3, high LSE. The vegetation of each sand encroachment level was projected on MFA (multiple factor analysis) dimensions using ten vectors representing different plant characteristics.

4 Discussion

After characterizing the vegetation cover to water stress in hot and arid environments (Boualala et al., 2020), this study shed light on plant communities of the desert pavements, which are one of the most characteristic landscapes of the Sahara Desert. In the Sahara Desert, the vegetation cover with geomorphological determinism, is closely linked to the habitat. Apart from the wadis and dry valleys that are colonized by plant groups, erg, Hamada- and Reg-type habitats have a low floristic diversity.

4.1 Evaluation of taxonomic diversity

The study area shelters 19 plant species belonging to 18 genera and 13 families, dominated in particular by *A. articulata* with rare species *D. scoparia*, *R. raetam*, and *S. pungens*. The floristic composition and abundance vary according to LSE, with a more marked representation of *A. articulata* in LLSE, *T. microphylla* in MLSE, and *C. saharae* in HLSE. On the other hand, the distribution of botanical families at different LSE is favoring the families of Asteraceae (richer in genera), Poaceae, Fabaceae, Scrophulariaceae, Amaranthaceae, and Thymeleaceae compared with Apiaceae. The same families are reported in previous studies in arid and semi-arid North Africa (Bouallala, 2013; Gamoun et al., 2018; Senoussi et al., 2021; Souahi et al., 2022). According to Heywood (1978), these families are not only restricted to arid environments, but they are the largest families of flowering plants in the world. According to Giulietti et al. (1987), the predominance of these families reflects their establishment ability in habitats with high solar radiation, shallow soils, steep slopes, and major factors of low availability of water and nutrients in these ecosystems. It also indicates their effective strategies of wind dispersal of their diaspores (Al-Shaye et al., 2020).

With regard to the distribution of 19 species identified, the range fluctuates between 10 in

LLSE and HLSE, and 14 species in MLSE, with dominance of ubiquitous and common species, such as *A. articulata*, *C. forsskaolii*, *M. halimifolius*, and *T. microphylla*. However, some species showed some exclusivity such as *S. acutiflora* in LLSE, *E. guyoniana* and *R. raetam* in MLSE, and *D. scoparia*, *E. alata*, *C. saharae*, and *S. pungens* in HLSE. In active sand dune fields and sandy habitats, species composition is associated with spatial heterogeneity and dynamics that can be determined by aeolian erosion, sand accumulation, and siltation (Nash et al., 1999; van Bodegom et al., 2004; Azizi et al., 2021).

The low vegetation cover characterizing hot and arid environments, especially in the Sahara Desert, prompts to apply purposive sampling technique in the study area, but the greater the sampling effort is, the more the number of species is expected to increase (Colwell and Elsensohn, 2014). At the beginning, the collection includes the most common species, and then increasingly rare species. In this study, the total number of observed species was 19, varying from 10 to 14 species depending on LSE. The use of non-parametric estimators revealed that there is a difference between observed richness and that estimated both for the area as a whole and for each LSE. For 4 estimators applied (Chao1, Chao2, Jack1, and Jack2), additional sampling effort is required to complete the inventory of missing rare species. In the study area as a whole, this additional sampling is estimated at 7% (Chao1), 23% (Chao2), 16% (Jack1), and 27% (Jack2). However, these predictions vary according to LSE. In LLSE, with its 11 observed species, the increase was 6% for Chao1, 7% for Chao2, 18% for Jack1, and 23% for Jack2. In MLSE (S_{obs}=14), the increase was 30% for Chao1, 10% for Chao2, 19% for Jack1, and 25% for Jack2. Finally, in HLSE (S_{obs}=10), the increase was 9% for Chao1, 2% for Chao2, 14% for Jack1, and 13% for Jack2. In any case, regardless of estimator used, the sampling effort turned out to be relatively insufficient. Although the Jackknife's estimator is known for its robustness (Colwell and Elsensohn, 2014), the values obtained are not far from the other estimators.

At 150 samples (10 times more than the reference sample) and independently of LSE, the observed richness (19 species) would reach 24 species, i.e., an increase of 29% for a number of individuals of 5910. In LLSE (S_{obs}=11, n=224 individuals), at 150 samples (30 times more than the reference sample), the number of estimated species (S_{est}) would be 12.80 for n=6720. For MLSE (S_{obs}=14, n=217), the predicted richness would reach 17.00 species for n=6510 individuals. For HLSE (S_{obs}=10, n=150), the estimated richness would be 10.53 species for 4500 individuals. Although there is a difference between observed and estimated species richness with different estimators applied, the missing sampling effort is not great, since the extrapolation curves reveal a plateau very quickly even before reaching the 20th sample or a little more, regardless of LSE.

By comparing the plant communities recorded at desert pavement with different LSE, a dissimilarity is reported among LLSE, MLSE, and HLSE. This species compositional dissimilarity may be due to the effect of native plants to form nabkhas following the trapping of mobile aeolian sediments and sand accumulations (Al-Dousari et al., 2008; Ahmed et al., 2015). As for vegetation parameters, the low rate of cover (14%–16%) accompanied by a decreasing abundance with the increase in LSE, represents a main indicator of climatic aridity in hot environments (Brovkin, 2002). As vegetation is the major component determining the nature of ecosystems (Orshan, 1986), its distribution is modulated by water availability and habitat quality (Munoz-Reinoso and Novo, 2005; Bouallala et al., 2022). On the other hand, the diversity indices (*H'*, *E*, and SRI) showed high values with a tendency to balance in MLSE and HLSE vs. low values in LLSE. According to Mota et al. (2018), the high values of diversity in these habitats could be explained by the installation of herbaceous and shrubby communities, which vary according to the landform, microclimate, soil depth, generating a mosaic character to this vegetation. According to Batanouny (1973), local topography not only controls water, but also affects its physical and chemical attributes. A slight depression of a few centimeters can lead to the accumulation of a thin layer of soil/sand transported by the water and/or wind, which contributes to the creation of a relatively favorable habitat to the growth of plants, despite the hostile desert conditions (Batanouny and Hilli, 1973).

4.2 Evaluation of plant functional diversity

According to Wang et al. (2018), plant functional traits provide information about adaptations to climate and environmental conditions, and can be used to explore the existence of alternative plant strategies within ecosystems. The analysis of plant ecological groups highlighted the predominance of psammophytes and a low quantity of gypsovag plants (gypsicoles or gypsophytes), and ruderals in LLSE and HLSE, while MLSE is colonized by saxicolous species. This diversity of ecological groups is linked to the nature of the soil, in particular particle size composition in sand. Moreover, the analysis of the rarity/abundance status of the flora showed good representations of C and CC types. Whereas CCC, AC, and R plants are poorly represented and less abundant.

Active dunes, whether continental or marine, are unfavorable for the survival of most plants due to the instability of the support except for psammophytes (Kent et al., 2005; Azizi et al., 2021). The latter are defined as the pioneering dune plant species (Liu et al., 2007). Therefore, only psammophytes adapting to wind–sand activity are established (Yan et al., 2007; Azizi et al., 2021). Topographic depressions serve as vegetation islands, composed of psammophytes and non-psammophytes (Yan et al., 2005), among which endemic or rare species occur (Groom et al., 2007). In all cases, vegetation distribution is scale-dependent. However, sand dune encroachment and wind–sand activity (sand burial and erosion) also contribute to shaping vegetation pattern (Liu et al., 2007; Azizi et al., 2021). Vegetation pattern is very likely to be associated with the scale level (Bossuyt and Hermy, 2004; Merdas et al., 2021). Microheterogeneity regulates erosion and soil nutrient distribution, and causes small-scale vegetation heterogeneity (Liu et al., 2007; Chenchouni, 2012). Observed vegetation patterns frequently reflect differences of natural conditions (Munoz-Reinoso and Novo, 2005).

Lifeform composition of plant community is a faithful indicator of adaptations of its constituent species to climatic conditions (Jamir and Pandey, 2003). Since phanerophytes prefer humid climates, such as equatorial regions (Raunkiær, 1934), and while chamaephytes indicate a temperate phytoclimate (Sophia et al., 2019), the dominance of therophytes in any region indicates an arid climate and disturbed habitat (Macheroum et al., 2021). Unlike some studies on the vegetation of arid and semi-arid environments, where therophytes dominated the lifeform spectrum (Bouallala, 2013; Neffar et al., 2018, Bouallala et al., 2020), this study showed that chamaephytes dominated in desert pavements invaded by aeolian sand deposits. Regardless of LSE, chamaephyte propositions exceeded the percentages of hemicryptophytes, therophytes, and phanerophytes. Therophytes are weakly present in the studied desert pavements, although the vegetation sampling was carried out during the optimal period of plant growth (February–April). This is in disagreement to plant biological spectra established in other arid and semi-arid zones of Algeria (Neffar et al., 2018; Bouallala et al., 2020). This biological type is dependent on rainfall (Abd El-Ghani et al., 2017). According to Harrison et al. (2010), therophytes are generally dominant in some of the planet's driest and coldest environments. This lifeform can be rare due to a combination of short growing seasons and low nutrient inputs to rock surfaces that prevent rapid establishment and growth (Ribeiro et al., 2007). It is most likely that their low presence in desert pavement with gravels and different LSE is associated with the instability of physical support resulting from the dominance of sandy soil texture (Bouzekri et al., 2023). In arid environments of the Middle East, Al-Shaye et al. (2020) reported that the dominance of therophytes and chamaephytes over other plant lifeforms is a response to the hyper-arid climate with insufficient rainfall; whereas some microhabitats can support a high percentage of perennials.

The large representation of chamaephytes can be explained by plant adaptations to adverse weather conditions (dry winters), with protected buds on the soil surface and/or by scales and leaves (Caiafa and Silva, 2005). The predominance of this biological type in the Saharan environments has already been reported by other studies (Chenchouni, 2012, Bradai et al., 2015, Gamoun et al., 2018). As for hemicryptophytes, unlike the results of Bouallala (2013) and Bouallala et al. (2020), their low representation in the vegetation studied in desert pavement with

gravels, would probably be attributed to overgrazing in this rangeland. In any case, their low abundance reduces competition for soil moisture to the benefit of chamaephytes (Gamoun et al., 2012, 2018). According to Rana et al. (2002), the low presence of hemicryptophytes indicates the effects of biotic factors on vegetation. While therophytes are typical of ruderal habitats, hemicryptophytes and phanerophytes require less disturbed habitats (Monteiro et al., 2012). Represented by two species (*E. alata* and *Retama retam* (Forssk.) Webb) in studied desert pavements, phanerophytic plants are a rare lifeform type in the Sahara Desert (Gamoun et al., 2018; Bouallala et al., 2020) except in habitats benefiting from a supply of water such as the case of valleys and wadi beds (Bradai et al., 2015). These two xerophytes are pioneers of mobile and semi-stable sand dunes in deserts and steppes (Barakat et al., 2013; Gorai et al., 2015).

With regard to plant longevity and response to the xericity of climate, perennials dominate in the study area. These plants implement a set of morphological, physiological, and anatomical adaptation mechanisms to ensure slow survival in life during long periods of drought (Gorai et al., 2015; Fatmi et al., 2020; Peguero-Pina et al., 2020). As a result, these are less subject to seasonal variations, constituting the only rangelands still available in the hot-dry season (Chehma, 2005; Bouallala, 2013). However, the variation in life forms reflects species-specific responses to environmental variations, and represents functional traits of the species that may be an important driver of ecosystem functioning (Pausas and Austin, 2001).

The studied plants generally adopt a dispersal mode of anemochoric, barochoric, then zoochoric type in desert pavement with aeolian sand deposits. The importance of wind in desert environments no longer needs to be demonstrated (Bradai et al., 2015; Bouallala et al., 2020). Wind dispersal reaches a peak synchronized with the dry season in Mediterranean (Navarro et al., 2009), desert (van Rooyen et al., 1990), and dry tropical (Griz and Machado, 2001) climates. In contrast, zoochory is the most dominant dispersal mechanism in dry and humid forests, and it decreases in ecosystems with dry climates (Genty, 1982), reflecting the low presence of mammals in the hostile desert conditions (Shabana et al., 2018). Finally, barochory is significant in temperate areas (Wang et al., 2009). Gentry (1982) and Jara-Guerrero et al. (2011) suggest that dispersal mechanisms may be associated with climatic factors and most likely with temporal patterns of water availability. These factors have the greatest impact on plant propagation in hyper-arid hot deserts (Griz and Machado, 2001). Plant dispersal strategy plays an essential role in the colonization of new habitats, population dynamics, species interactions, community structures, and plant diversity (Morales and Carlo, 2006). It can be considered as a key factor in the conservation biology and restoration planning (Jara-Guerrero et al., 2011).

Our findings revealed that arido-active plants exceed arido-passives. According to Jauffret (2001), arido-active species have water reserves to function. These plants benefit from sandy soils, which are capable of creating edapho-climatic conditions, favoring the development of a specific plant cover. The evolution of proportions of arido-active and arido-passive plants in the plant populations of dry zones could provide information on the vulnerability and/or the resilience capacity of ecosystems in the face of aridity and consequently climate change. The regression of arido-actives could reflect a trend towards aridification. While all annuals (therophytes) are arido-passive, perennial species are not always arido-active (Neffati et al., 2016; Neffar et al., 2022). The same is true for Grime's strategy, which competitive, stress-tolerant plants, and stress-tolerators predominate other classes. Generally, even after the destruction of aerial phytomass, long-lived plants (competitive and stress-tolerant plants) will be able to sprout after grazing or cutting wood (Jauffret, 2001). With regard to the chorology of identified species, plants with the Saharo-Arabic chorological type predominated throughout the study area with Mediterranean Saharo-Arabic type and endemic to the Algerian-Moroccan Sahara. These are the phytogeographic types best suited to the Saharan environments (Guinet and Sauvage, 1954; Quézel, 1965; Salama et al., 2014; Bouallala et al., 2020). Plants with the Mediterranean Saharo-Arabian chorological types find in MLSE, a favorable environment to develop and thrive. The endemic plants to the Algerian-Moroccan Sahara, despite their low presence and abundance, have managed to develop and spread in desert pavements of the Algerian Sahara Desert.

5　Conclusions

Based on the climatic and geomorphological characteristics, desert pavements of the northern Sahara represent hyper-arid environments with low vegetation cover and plant diversity. The analysis of this floristic diversity in the desert pavements gave insightful indicators on the state of evolution of the Saharan ecosystem through the presence and abundance of so-called exclusive species, which are good indicators of soils and sub-surface substrates. The present study showed that LLSE is characterized by an exclusive species, MLSE by two exclusive species, and HLSE by four exclusive species. The lifeform type best adapted to the environmental conditions of sandy desert pavements is chamaephytes. Generally, the dispersion of the majority of plants that constitute the phytocenoses analyzed is ensured by anemochory. Competitive and stress-tolerant plants are dominant and are able to sprout after grazing or cutting of aerial parts. Despite the diversity of chorological types, the Saharo-Arabian type remains by far the best represented and the best adapted to the conditions of sandy desert pavement of the Sahara Desert. Psammophytes dominate in the community of desert pavement despite the diversity of soil substrates. Furthermore, it is necessary to extend this study to other types of ecosystems to better understand the evolution and dynamics of biodiversity in hot and arid regions, especially the Sahara Desert.

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References

Abd El-Ghani M M A, Huerta-Martínez F M, Hongyan L, et al. 2017. Plant Responses to Hyperarid Desert Environments. Cham: Springer, 598.

Ahmed M, Al-Dousari N, Al-Dousari A. 2015. The role of dominant perennial native plant species in controlling the mobile sand encroachment and fallen dust problem in Kuwait. Arabian Journal of Geosciences, 9(2): 134, doi: 10.1007/s12517-015-2216-6.

Al-Dousari A M, Ahmed M, Al-Senafy M, et al. 2008. Characteristics of nabkhas in relation to dominant perennial plant species in Kuwait. Kuwait Journal of Science and Engineering, 35(1): 129–150.

Al-Dousari A M, Ahmed M, Al-Dousari N, et al. 2019. Environmental and economic importance of native plants and green belts in controlling mobile sand and dust hazards. International Journal of Environmental Science and Technology, 16(5): 2415–2426.

Al Shaye N A, Masrahi Y S, Thomas J. 2020. Ecological significance of floristic composition and life forms of Riyadh region, Central Saudi Arabia. Saudi Journal of Biological Sciences, 27(1): 35–40.

Arar A, Chenchouni H. 2012. How could geomatics promote our knowledge for environmental management in Eastern Algeria? Journal of Environmental Science and Technology, 5(5): 291–305.

Arar A, Chenchouni H. 2014. A "simple" geomatics-based approach for assessing water erosion hazard at montane areas. Arabian Journal of Geosciences, 7(1): 1–12.

Audru J, Cesar J, Lebrun J P. 1994. The Vascular Plants of the Republic of Djibouti. Volume I. Montpellier: CIRAD–EMVT, 29–45. (in French)

Azizi M, Chenchouni H, Belarouci M E H, et al. 2021. Diversity of psammophyte communities on sand dunes and sandy soils of the northern Sahara Desert. Journal of King Saud University–Science, 33(8): 101656, doi: 10.1016/j.jksus.2021.101656.

Barakat N A, Laudadio V, Cazzato E, et al. 2013. Potential contribution of *Retama raetam* (Forssk.) Webb & Berthel as a forage shrub in Sinai, Egypt. Arid Land Research and Management, 27(3): 257–271.

Batanouny K H. 1973. Soil properties as affected by topography in desert wadis. Acta Botanica Academiae Scientiarum Hungaricae, 19: 13–21.

Batanouny K H, Hilli M R. 1973. Phytosociological study of Ghurfa Desert, central Iraq. Phytocoenologia, 1: 223–249.

Benabderrahmane M C, Chenchouni H. 2010. Assessing environmental sensitivity areas to desertification in Eastern Algeria using Mediterranean desertification and land use "MEDALUS" model. International Journal of Sustainable Water and Environmental Systems, 1(1): 5–10.

Benhouhou S S, Dargie T C D, Gilbert O L. 2001. Vegetation associations in the Great Western Erg and the Saoura Valley, Algeria. Phytocoenologia, 31(3): 311–324.

Bossuyt B, Hermy M. 2004. Seed bank assembly follows vegetation succession in dune slacks. Journal of Vegetation Science, 15(4): 449–456.

Bouallala M. 2013. Floristic and nutritive spatio-temporal study of the camel rangelands of the Algerian Western Sahara: Case of the regions of Béchar and Tindouf. PhD Dissertation. Ouargla: University of Ouargla. (in French)

Bouallala M, Neffar S, Chenchouni H. 2020. Vegetation traits are accurate indicators of how do plants beat the heat in drylands: Diversity and functional traits of vegetation associated with water towers in the Sahara Desert. Ecological Indicators, 114: 106364, doi: 10.1016/j.ecolind.2020.106364.

Bouallala M, Bradai L, Chenchouni H. 2022. Effects of sand encroachment on vegetation diversity in the Sahara Desert. In: Chenchouni H, Chaminé H I, Khan M F, et al. New Prospects in Environmental Geosciences and Hydrogeosciences. Cham: Springer, 133–138.

Bouarfa S, Bellal S A. 2018. Assessment of the aeolian sand dynamics in the region of Ain Sefra (Western Algeria), using wind data and satellite imagery. Arabian Journal of Geosciences, 11: 56, doi: 10.1007/s12517-017-3346-9.

Bouchlaghem K, Chtioui H, Gazzah M H. 2021. Analyzing the impact of Saharan sand and dust storms based on HYSPLIT algorithm in Tunisian regions. Arabian Journal of Geosciences, 14: 834, doi: 10.1007/s12517-021-07174-4.

Bradai L, Bouallala M H, Bouziane N F, et al. 2015. An appraisal of eremophyte diversity and plant traits in a rocky desert of the Sahara. Folia Geobotanica, 50(3): 239–252.

Bouzekri A, Alexandridis T K, Toufik A, et al. 2023. Assessment of the spatial dynamics of sandy desertification using remote sensing in Nemamcha region (Algeria). The Egyptian Journal of Remote Sensing and Space Sciences, 26. (in Press)

Brovkin V. 2002. Climate-vegetation interaction. Journal de Physique IV, 12(10): 57–72.

Caiafa A N, Silva A F D. 2005. Floristic composition of a "Campo de Altitude" in the Sierra do Brigadeiro state park, Minas Gerais-Brazil. Rodriguésia, 56(87): 163–173.

Chao A, Chazdon R L, Colwell R K, et al. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters, 8(2): 148–159.

Chehma A. 2005. Spatio-temporal floristic and nutritive study of camel rangelands in the northern Algerian Sahara. Case of the Ouargla and Ghardaia regions. PhD Dissertation. Annaba: University of Annaba. (in French)

Chenchouni H. 2012. Flora diversity of a lake at Algerian Low-Sahara. Acta Botanica Malacitana, 37: 33–44.

Chenchouni H, Errami E, Rocha F, et al. 2019. Exploring the Nexus of Geoecology, Geography, Geoarcheology and Geotourism: Advances and Applications for Sustainable Development in Environmental Sciences and Agroforestry Research. Cham: Springer, 109.

Chenchouni H, Chaminé H I, Khan M F, et al. 2022. New Prospects in Environmental Geosciences and Hydrogeosciences. Cham: Springer, 635.

Colwell R K, Elsensohn J E. 2014. EstimateS turns 20: Statistical estimation of species richness and shared species from samples. Ecography, 37(6): 609–613.

Copeland S M, Bradford J B, Duniway M C, et al. 2017. Potential impacts of overlapping land-use and climate in a sensitive dryland: a case study of the Colorado Plateau, USA. Ecosphere, 8(5): e01823, doi: 10.1002/ecs2.1823.

Coude-Gaussen G. 2002. Surface formations of hot deserts and their margins. In: Miskovsky J C. Geology of Prehistory. Paris: Presses Universitaires de Perpignan, 125–144. (in French)

Dadamoussa M L, Senoussi A, Idder M A, et al. 2015. Small development in the Algerian northern Sahara: Between development policies and reality, case of Ouargla, Ghardaïa and El-Oued. Livestock Research for Rural Development, 27(10): 210. (in French)

Dashti A, Mohammad R, Al-Hurban A. 2021. Sand dunes-induced geomorphological changes in Um Ar-Rimam depression, Kuwait. Arabian Journal of Geosciences, 14: 1632, doi: 10.1007/s12517-021-08108-w.

Dewitte O, Jones A, Spaargaren O, et al. 2013. Harmonisation of the soil map of Africa at the continental scale. Geoderma, 211–212: 138–153.

Dubief J. 1959. The Climate of the Sahara. Volume I. Temperature. Alger: Travaux de l'Institut de Recherche Saharienne, 312. (in French)

Dubief J. 1963. The Climate of the Sahara. Volume II. Precipitation. Alger: Travaux de l'Institut de Recherche Saharienne, 275. (in French)

Fabre J. 2005. Geology of Western and Central Sahara. Tervuren: Royal Museum for Central Africa, 19. (in French)

FAO. 2014. Training manual for combating desertification, dune fixation and afforestation management in Mauritania. Nouakchott. [2022-08-16]. https://www.apefe.org/component/docman/cat_view/141-manuel.html. (in French)

Fatmi H, Mâalem S, Harsa B, et al. 2020. Pollen morphological variability correlates with a large-scale gradient of aridity. Web Ecology, 20(1): 19–32.

Faurie C, Ferra C, Medori P, et al. 2003. Ecology: Scientific Approches and Practice. Paris: Tec & Doc, 488. (in French)

Fu Q, Feng S. 2014. Responses of terrestrial aridity to global warming. Atmospheres, 119(13): 7863–7875.

Gamoun M, Ouled Belgacem A, Hanchi B, et al. 2012. Impact of grazing on the floristic diversity of arid rangelands in South Tunisia. Revue Ecologie (Terre Vie), 67(3): 271–282

Gamoun M, Belgacem A O, Louhaichi M. 2018. Diversity of desert rangelands of Tunisia. Plant Diversity, 40(5): 217–225.

Gentry A H. 1982. Patterns of neotropical plant species diversity. In: Hecht M K, Wallace B, Prance G T. Evolutionary Biology. Boston: Springer, 1–84.

Giulietti A M, de Menezes N L, Pirani J R, et al. 1987. Flora of Serra do Cipó, Minas Gerais: Characterization and list of species. Boletim de Botânica da Universidade de São Paulo, 9: 151, doi: 10.11606/issn.2316-9052.v9i0p1-151. (in Portuguese)

Gorai M, Laajili W, Santiago L S, et al. 2015. Rapid recovery of photosynthesis and water relations following soil drying and re-watering is related to the adaptation of desert shrub *Ephedra alata* subsp. *alenda* (Ephedraceae) to arid environments. Environmental and Experimental Botany, 109: 113–121.

Grime J P, Hodgson J G, Hunt R. 1988. Comparative Plant Ecology: A Functional Approach to Common British Species. Dordrecht: Springer, 742.

Griz L M S, Machado I C S. 2001. Fruiting phenology and seed dispersal syndromes in Caatinga, a tropical dry forest in the northeast of Brazil. Journal of Tropical Ecology, 17(2): 303–321.

Groom J D, McKinney L B, Ball L C, et al. 2007. Quantifying off-highway vehicle impacts on density and survival of a threatened dune-endemic plant. Biological Conservation, 135(1): 119–134.

Guinet P H, Sauvage C H. 1954. South Moroccan Hamadas, Botanical Series. Hamadas: Cherifian Scientific Institute, 75–167. (in French)

Hall R M, Penke N, Kriechbaum M, et al. 2020. Vegetation management intensity and landscape diversity alter plant species richness, functional traits and community composition across European vineyards. Agricultural Systems, 177: 102706, doi: 10.1016/j.agsy.2019.102706.

Harrison S P, Prentice I C, Barboni D, et al. 2010. Ecophysiological and bioclimatic foundations for a global plant functional classification. Journal of Vegetation Science, 21(2): 300–317.

Heywood V H. 1978. Flowering Plants of the World. Oxford: Oxford University Press, 33.

Hughes L, Dunlop M, French K, et al. 1994. Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. Journal of Ecology, 82: 933–950.

Jamir S A, Pandey H N. 2003. Vascular plant diversity in the sacred groves of Jaintia Hills in northeast India. Biodiversity & Conservation, 12(7): 1497–1510.

Jaouen X. 1988. Trees, Shrubs and Bushes of Mauritania. Nouakchott: CCF, 31. (in French)

Jara-Guerrero A, de la Cruz M, Méndez M. 2011. Seed dispersal spectrum of woody species in south Ecuadorian dry forests: Environmental correlates and the effect of considering species abundance. Biotropica, 43(6): 722–730.

Jauffret S. 2001. Validation and comparison of various indicators of long-term changes in arid Mediterranean ecosystems: Application to the monitoring of desertification in southern Tunisia. PhD Dissertation. Marseille: University of Aix-Marseille III. (in French)

Kent M, Owen N W, Dale M P. 2005. Photosynthetic responses of plant communities to sand burial on the Machair dune systems of the Outer Hebrides, Scotland. Annals of Botany, 95(5): 869–877.

Kouba Y, Merdas S, Mostephaoui T, et al. 2021. Plant community composition and structure under short-term grazing exclusion in steppic arid rangelands. Ecological Indicators, 120: 106910, doi: 10.1016/j.ecolind.2020.106910.

Lavorel S, Diaz S, Cornelissen J H C, et al. 2007 Plant functional types: are we getting any closer to the Holy Grail? In: Canadell J G, Pataki D E, Pitelka L F. Terrestrial Ecosystems in a Changing World. Heidelberg: Springer, 149–164.

Le Houérou H N. 1990. Definition and bioclimatic limits of the Sahara. Sécheresse, 1(4): 246–259. (in French)

Lemee G. 1953. Contribution to phytosociological knowledge of the Saharo-Moroccan confines: Therophyte associations of sandy and non-salte loamy depressions and rockeries around Beni-Ounif. Vegetatio, 4(3): 137–154. (in French)

Liu Z, Li X, Yan Q, et al. 2007. Species richness and vegetation pattern in interdune lowlands of an active dune field in Inner Mongolia, China. Biological Conservation, 140(1–2): 29–39.

Macheroum A, Kadik L, Neffar S, et al. 2021. Environmental drivers of taxonomic and phylogenetic diversity patterns of plant communities in semi-arid steppe rangelands of North Africa. Ecological Indicators, 132: 108279, doi: 10.1016/j.ecolind.2021.108279.

Macheroum A, Chenchouni H. 2022. Short-term land degradation driven by livestock grazing does not affect soil properties in semiarid steppe rangelands. Frontiers in Environmental Science, 10: 846045, doi: 10.3389/fenvs.2022.846045.

Merdas S, Kouba Y, Mostephaoui T, et al. 2021. Livestock grazing-induced large-scale biotic homogenization in arid Mediterranean steppe rangelands. Land Degradation & Development, 32(17): 5099–5107.

Mihi A, Tarai N, Chenchouni H. 2019a. Can palm date plantations and oasification be used as a proxy to fight sustainably against desertification and sand encroachment in hot drylands?. Ecological Indicators, 105: 365–375.

Mihi A, Nacer T, Chenchouni H. 2019b. Monitoring dynamics of date palm plantations from 1984 to 2013 using Landsat Time-Series in Sahara Desert Oases of Algeria. In: El-Askary H M, Lee S, Heggy E, et al. Advances in Remote Sensing and Geo Informatics Applications. Cham: Springer, 225–228.

Monod T. 1992. Desert. Sécheresse, 3(1): 7–24. (in French)

Monteiro A, Caetano F, Vasconcelos T, et al. 2012. Vineyard weed community dynamics in the Dão winegrowing region. Ciência e Técnica Vitivinicola, 27(2): 73–82.

Morales J M, Carlo T A. 2006. The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. Ecology, 87(6): 1489–1496.

Mota G S, Luz G R, Mota N M, et al. 2018. Changes in species composition, vegetation structure, and life forms along an altitudinal gradient of rupestrian grasslands in south-eastern Brazil. Flora, 238: 32–42.

Munoz-Reinoso J C, Novo F G. 2005. Multiscale control of vegetation patterns: The case of Doñana (SW Spain). Landscape Ecology, 20(1): 51–61.

Nash M S, Whitford W G, de Soyza A G, et al. 1999. Livestock activity and Chihuahuan Desert annual-plant communities: boundary analysis of disturbance gradients. Ecological Applications, 9(3): 814–823.

Navarro T, Pascual V, Alados C L, et al. 2009. Growth forms, dispersal strategies and taxonomic spectrum in a semi-arid shrubland in SE Spain. Journal of Arid Environments, 73(1): 103–112.

Neffar S, Chenchouni H, Si Bachir A. 2016. Floristic composition and analysis of spontaneous vegetation of Sabkha Djendli in North-east Algeria. Plant Biosystems, 150(3): 396–403.

Neffar S, Menasria T, Chenchouni H. 2018. Diversity and functional traits of spontaneous plant species in Algerian rangelands rehabilitated with prickly pear (*Opuntia ficus-indica* L.) plantations. Turkish Journal of Botany, 42(4): 448–461.

Neffar S, Beddiar A, Menasria T, et al. 2022. Planting prickly pears as a sustainable alternative and restoration tool for rehabilitating degraded soils in dry steppe rangelands. Arabian Journal of Geosciences, 15(3): 287.

Neffati M, Sghaier M, Labbene Y. 2016. Meeting the challenges of climate change through adaptation and mitigation. Project OSS-MENA-DELP. [2022-07-15]. https://www.profor.info/sites/profor.info/files/Rapport%20principal-Etude%20CC-MENA.PDF. (in French)

Negre R. 1962. Small Flora of the Arid rRegions of Western Morocco. Paris: CNRS, 34. (in French)

Noy-Meir I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology, Evolution, and Systematics, 4: 25–51.

Orshan G. 1986. The deserts of the Middle East. In: Evenari M, Noy-Meir I, Goodall D W. Hot Deserts and Arid Shrublands. Amsterdam: Elsevier, 1–28.

Ozenda P. 1991. Flora and Vegetation of the Sahara. Paris: CNRS, 660. (in French)

Ozenda P. 2004. Flora and Vegetation of the Sahara. Paris: CNRS, 662. (in French)

Parsons A J, Abrahams A D. 2009. Geomorphology of Desert Environments. Dordrecht: Springer, 831.

Pausas J G, Austin M P. 2001. Patterns of plant species richness in relation to different environments: an appraisal. Journal of Vegetation Science, 12(2): 153–166.

Peguero-Pina J J, Vilagrosa A, Alonso-Forn D, et al. 2020. Living in drylands: Functional adaptations of trees and shrubs to cope with high temperatures and water scarcity. Forests, 11(10): 1028, doi: 10.3390/f11101028.

Pielou E C. 1975. Ecological Diversity. New York: Wiley InterScience, 166.

Quézel P, Santa S. 1962. New Flora of Algeria and the Southern Desert Regions. Volume 1. Paris: CNRS, 1–565. (in French)

Quézel P, Santa S. 1963. New Flora of Algeria and the Southern Desert Regions. Volume 2. Paris: CNRS, 566–1170. (in French)

Quézel P. 1965. The Vegetation of the Sahara from Chad to Mauritania. Stuttgart: Gustav Verlag, 333. (in French)

Quézel P. 1978. Analysis of the flora of Mediterranean and Saharan Africa. Annals of the Missouri Botanical Garden, 65(2): 479–534.

Rana T S, Datt B, Rao R R. 2002. Life forms and biological spectrum of the flora of Tons valley, Garhwal Himalaya (Uttaranchal), India. Taiwania, 47(2): 164–169.

Raunkiær C. 1934. The Life-forms of Plants and Statistical Plant Geography. Oxford: Clarendon Press, 632.

Ribeiro K T, Medina B M O, Scarano F R. 2007. Species composition and biogeographic relations of the rock outcrop flora on

the high plateau of Itatiaia, SE-Brazil. Brazilian Journal of Botany, 30(4): 623–639.

Salama F, Abd El-Ghani M, Gadallah M, et al. 2014. Variations in vegetation structure, species dominance and plant communities in South of the Eastern Desert-Egypt. Notulae Scientia Biologicae, 6(1): 41–58.

Seltzer P. 1946. The Climate of Algeria. Algiers: University of Algiers, 24. (in French)

Senoussi A, Schadt I, Hioun S, et al. 2021. Botanical composition and aroma compounds of semi-arid pastures in Algeria. Grass and Forage Science, 76(2): 282–299.

Shameem S A, Mushtaq H, Wani A A, et al. 2017. Phytodiversity of herbaceous vegetation in disturbed and undisturbed forest ecosystems of Pahalgam valley, Kashmir Himalaya, India. British Journal of Environment & Climate Change, 7(3): 148–167.

Sinsin T, Mounir F, El Aboudi A. 2021. Modeling and assessing driving factors of the spatial and temporal dynamics of the sand dunes in the district of Errachidia, Morocco. Arabian Journal of Geosciences, 14: 2111, doi: 10.1007/s12517-021-08423-2.

Sirvent L. 2020. Biological Types: State of the Art, Updating of Definitions and Establishment of a Repository. Porquerolles: National Mediterranean Botanical Conservatory of Porquerolles, 64. (in French)

Sophia M, Behera N, Gupta A. 2019. Life-form and biological spectrum of sub-tropical forests and agroecosystems of Manipur in North-east India. Pleione, 13(2): 346–354.

Souahi H, Gacem R, Chenchouni H. 2022. Variation in plant diversity along a watershed in the semi-arid lands of North Africa. Diversity, 14(6): 450, doi: 10.3390/d14060450.

Tanji A. 2005. Wheat and Barley Weeds in Morocco. Raba: INRA, 134. (in French)

van Bodegom P, Bakker C, van der Gon H D. 2004. Identifying key issues in environmental wetland research using scaling and uncertainty analysis. Regional Environmental Change, 4(2/3): 100–106.

van Der Pijl L. 1982. Principles of Dispersal in Higher Plants. Heidelberg: Springer, 218.

van Rooyen M W, Theron G K, Grobbelaar N. 1990. Life form and dispersal spectra of the flora of Namaqualand, South Africa. Journal of Arid Environments, 19(2): 133–145.

Violle C, Navas M L, Vile D, et al. 2007. Let the concept of trait be functional! Oikos, 116(5): 882–892.

von Maydell H J. 1983. Trees and Shrubs of the Sahel, their Characteristics and Uses. Eschbon: German Agency for Technical Cooperation, 517–531. (in French)

Wang H, Harrison S P, Prentice I C, et al. 2018. The China plant trait database: Toward a comprehensive regional compilation of functional traits for land plants. Ecology, 99(2): 500–500.

Wang J H, Baskin C C, Cui X L, et al. 2009. Effect of phylogeny, life history and habitat correlates on seed germination of 69 arid and semi-arid zone species from northwest China. Evolutionary Ecology, 23: 827–846.

Weiher E A, van der Werf, Thompson K, et al. 1999. Challenging Theophrastus: A common core list of plant trait for functional ecology. Journal of Vegetation Science, 10: 609–620.

Yan Q, Liu Z, Zhu J, et al. 2005. Structure, pattern and mechanisms of formation of seed banks in sand dune systems in northeastern Inner Mongolia, China. Plant and Soil, 277: 175–184.

Yan Q, Liu Z, Ma J, et al. 2007. The role of reproductive phenology, seedling emergence and establishment of perennial *Salix gordejevii* in active sand dune fields. Annals of Botany, 99(1): 19–28.

Yazdani M, Sobhani B, Zengir V S, et al. 2020. Analysis, monitoring and simulation of dust hazard phenomenon in the northern Persian Gulf, Iran, Middle East. Arabian Journal of Geosciences, 13: 530, doi: 10.1007/s12517-020-05470-z.
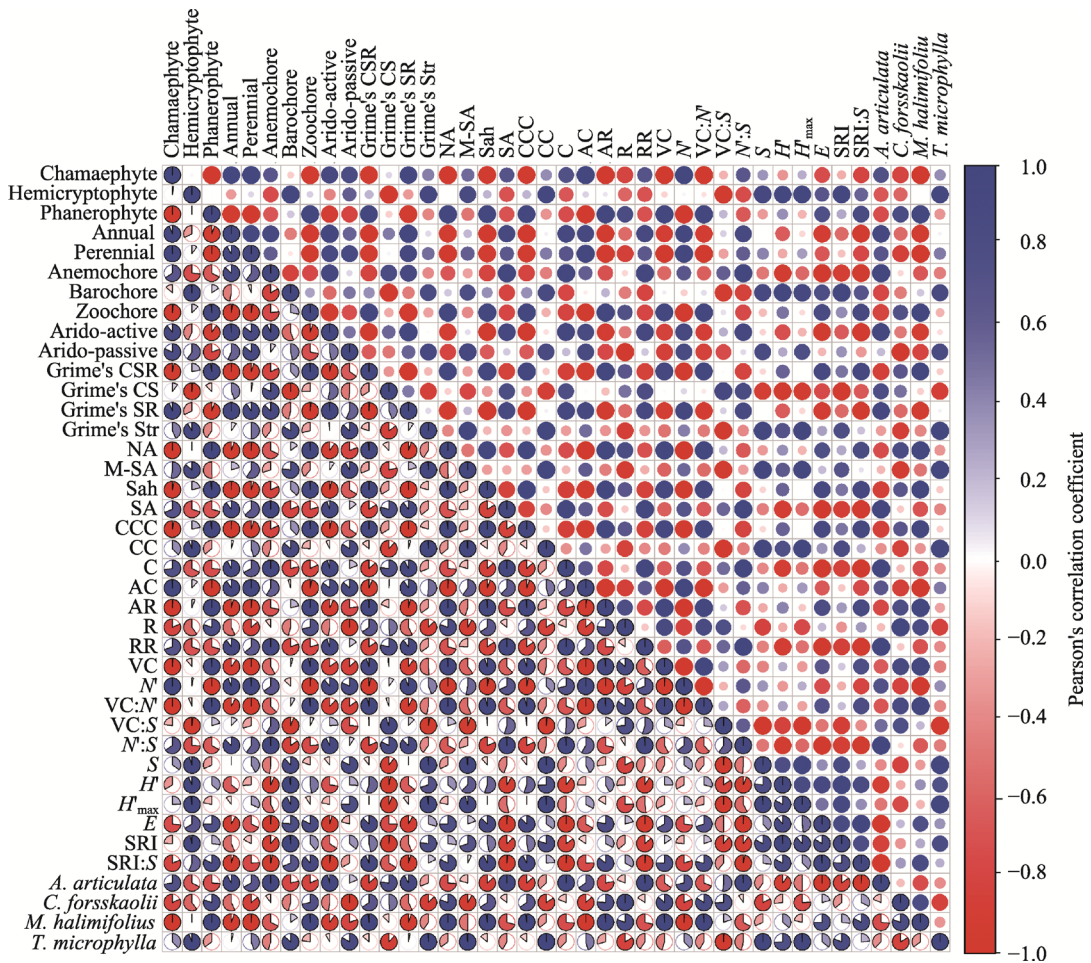
Appendix

Fig. S1 Pearson's correlation matrix between sub-levels of all plant variables clustered in the bi-plot of multiple factorial analysis (MFA). CSR, competition-stress-ruderality; CS, competition-stress; SR, stress-ruderality; Str, stress-tolerant; NA, North African chorological type; M-SA, Mediterranean-Saharo-Arabian; Sah, Saharan chorological type; SA, Saharo-Arabian; CCC, widespread; CC, very common; C, common; AC, fairly common; AR, quite rare; R, rare; RR, very rare; VC, vegetation cover; N', density; S, species richness; H', Shannon's diversity index; H'_{max} maximum Shannon's diversity index; E, Evenness index; SRI, Simpson's reciprocal index.

Table S1 Climatic information of the El-Guerrara region at the Ghardaia Province in the Sahara Desert of Algeria

Climatic information	Value/class
Latitude	32°46′N
Longitude	04°33′E
Altitude (m)	280
Koeppen's climate classification	BWh (B=Arid climate; W=Desert; h=hot)
Budyko's climate	Desert
Radiational index of dryness	35.662
Budyko's evaporation (mm/a)	40
Budyko's runoff (mm/a)	0
Budyko's evaporation (%)	100
Budyko's runoff (%)	0
Aridity	Hyper-arid
Aridity index	0.02
Moisture index (%)	−98
de Martonne's index	1
Precipitation deficit (mm/a)	1639
Climatic NPP (g DM/(m²·a))	79
NPP (Temperature)	2363
NPP (Precipitation)	79
NPP is precipitation limited	
Gorczynski's continentality index	51.7

Note: NPP, net primary production. DM, dry matter.

Table S2 Long-term monthly climatic data near the El-Guerrara region at the Ghardaia Province in the Sahara Desert of Algeria

Parameter	Jan	Feb	Mar	Apr	May	Jun	Jul
Mean temperature (°C)	11.1±1.38	13.6±1.20	16.8±1.50	21.0±0.95	25.7±1.63	31.2±1.46	33.7±1.54
Maximum temperature (°C)	17.2±3.66	20.0±3.94	23.2±4.15	28.8±4.31	32.7±4.22	39.4±4.40	42.7±4.64
Minimum temperature (°C)	4.4±3.24	6.6±3.64	9.3±4.29	13.8±4.95	17.7±4.99	23.2±5.80	25.5±5.62
Precipitation (mm)	7±3.44	5±2.11	8±2.10	1±3.85	1±2.62	0±3.16	0±1.20
Potential evapotranspiration (mm)	57±16.38	74±17.90	120±25.69	147±21.64	193±25.24	219±22.40	234±20.27
Water vapor pressure (hPa)	8.2±2.00	8.8±3.15	8.2±3.97	12.3±4.46	13.9±6.43	16.5±8.07	20.5±7.52
Wind speed (km/h)	7.2±4.19	7.9±4.83	7.2±5.33	9.0±5.14	9.0±4.79	8.6±4.61	7.2±3.14
Sunshine frequency (%)	67±9.64	73±7.44	74±9.13	72±9.94	70±4.57	67±4.65	80±1.85
Day length (h)	9.6	12.0	12.0	12.0	14.4	14.2	13.9
Sunshine hours (h)	7.2	7.2	9.6	9.6	9.6	9.6	11.3
Ground frost frequency (%)	13	5	0	0	0	0	0
Effective rainfall (mm)	7	5	8	1	1	0	0
Effective rainfall percentage (%)	99	99	99	100	100	100	100
Number of rainy days (d)	1	1	1	0	0	0	0
Solid precipitation ratio	2	1	0	0	0	0	0

Parameter	Aug	Sep	Oct	Nov	Dec	Average
Mean temperature (°C)	34.0±1.34	28.6±1.29	22.2±1.02	15.8±1.21	11.1±0.95	22.07±1.29
Maximum temperature (°C)	41.7±4.39	37.2±3.92	30.5±4.34	23.2±3.86	18.2±3.51	29.6±4.11
Minimum temperature (°C)	25.0±5.20	22.2±4.81	16.1±4.59	10.0±3.73	6.0±3.28	15.0±4.51
Precipitation (mm)	0±0.86	4±2.45	3±2.53	6±3.06	5±6.30	3±5.31
Potential evapotranspiration (mm)	228±20.63	172±15.29	125±18.01	62±15.80	47±12.78	140±19.34
Water vapor pressure (hPa)	21.8±8.21	19.7±5.11	15.3±2.66	13.7±3.25	9.6±1.97	14.0±4.73
Wind speed (km/h)	7.2±3.05	7.9±2.81	8.6±3.31	7.2±2.77	7.2±3.24	7.9±3.93
Sunshine frequency (%)	78±4.70	73±9.62	71±7.29	66±9.58	67±12.16	72±7.53
Day length (h)	13.2	12.0	12.9	9.6	9.6	12.0
Sunshine hours (h)	10.3	9.6	7.2	7.2	7.2	9.6
Ground frost frequency (%)	0	0	0	0	7	2
Effective rainfall (mm)	0	4	3	6	5	40
Effective rainfall percentage (%)	100	99	100	99	99	99
Number of rainy days (d)	0	0	0	1	1	5
Solid precipitation ratio	0	0	0	1	2	1

Note: mean±SD; LST, local standard time.